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VARIABILITY IN EXPERIMENTAL BAKING

II. THE INFLUENCE OF MECHANICAL MOULDING IN REDUCING THE VARIABILITY IN LOAF VOLUME BETWEEN LABORATORIES¹

By W. F. GEDDES,² R. K. LARMOUR³ AND J. G. MALLOCH⁴

Abstract

The results of replicate bakings of five flours by the simple and bromate formulas in three laboratories, using both hand and machine moulding, showed that differences in the manual manipulation of doughs during moulding by experienced operators are relatively unimportant in causing variability between replicates. Mechanical moulding slightly reduced the variability between laboratories but the mean volumes for the three laboratories fell in the same order for hand and machine moulding, indicating that certain systematic factors were operating which affected the hand and machine results similarly. Machine moulding slightly reduced the differences in mean loaf volume obtained by three bakers of varying experience working in the same laboratory, while in the instance of three experienced bakers, hand moulding gave the lower variability between bakers.

Introduction

In the first paper (1) of this series, the results of an extensive series of experiments, carried out with the Thomson laboratory model loaf moulder in the Cereal Chemical laboratory of the University of Manitoba in 1930, were presented. The experiments were designed to determine the value of mechanical moulding as compared with hand moulding in reducing (i), the variability between replicate bakings of the same flour by one operator, (ii) the variation within the same day and on different days, (iii) the variability between operators. With the most satisfactory adjustment of the mechanical moulder, mechanical moulding gave only a slightly lower variability in the loaf volume of replicate bakings than hand moulding, but the machine-moulded loaves were smaller in volume, coarser in texture and duller in crumb color. Machine moulding did not reduce the difference between days nor the trends in loaf volume within days. In fact, when the days were arranged in order of increasing mean loaf volume the same order was obtained by hand and machine moulding, indicating the operation of some systematic factors that influenced hand and machine results similarly. Experiments conducted by

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bakers of different degrees of experience gave results which indicated that inexperience in moulding is not an important factor contributing to variability between replicates. However, the personal element in both punching and moulding was found to contribute to the variability between bakers, individuality in moulding being somewhat the more important factor.

A study of the factors contributing to variability in experimental baking is of particular interest to the Associate Committee on Grain Research, National Research Council of Canada, since the experimental work in connection with the various projects of the Committee is replicated in the different laboratories co-operating with the Committee. While the standardization of the baking methods employed has resulted in fair relative agreement between the collaborating institutions, wide differences in the absolute values for any given flour are obtained.

Although individuality both in punching and moulding technique was found to contribute to the variability between operators in the Manitoba laboratory, the relatively greater importance of moulding technique indicated that the introduction of mechanical moulding might effect a significant reduction in the variability between laboratories. The studies reported in this paper were accordingly undertaken to secure information on this point.

Experimental

Upon completion of the tests in the Manitoba laboratory, the mechanical moulder was forwarded to the University of Saskatchewan, together with 50-lb. samples of the five flours that had been used by the former laboratory in the second series of experiments. A description of the flours is given in

TABLE I
DESCRIPTION OF FLOURS

Flour No.	Description	Bleaching treatment	Chemical analysis, 13.5% moisture basis	
			Protein, %	Ash, %
5	Commercially milled, 50% patent	Alsop (nitrogen peroxide) + $\frac{1}{4}$ oz. Novadel (benzoyl peroxide) per bbl.	12.3	0.39
6	Commercially milled, bottom 60%	Unbleached	14.0	0.60
7	Commercially milled, 96% patent	1.5 gm. Agene (nitrogen trichloride) per bbl. + Alsop	13.2	0.49
8	Commercially milled, 2nd clear (bottom 15%)	3 gm. Agene per bbl.	15.4	1.05
9	Experimentally milled, straight grade	None	13.9	—

Table I. After preliminary tests, these flours were baked by an experienced baker (A) by the simple and bromate formulas, using the same flour absorptions as the Manitoba laboratory. Fifty loaves of one flour were baked daily, the first 25 being hand moulded and the second 25 machine moulded, the adjustment of the moulder being that specified by the Manitoba laboratory, namely, the sheeting rolls set at "2" on the dial and the depth of the compression chamber at the upper end adjusted to 1.28 in. corresponding to a depth of 1.603 in. at the exit end, the latter measurement being made vertically to the drum.

In order to secure further information on the utility of mechanical moulding in reducing the variability between operators, flour Number 7 was also baked by two other operators, using the bromate formula, each baking 25 loaves by hand moulding and 25 by machine moulding. The moulder was then shipped to the University of Alberta where a similar series of experiments was carried out with samples of the same flours, thus providing comparative data for hand and machine moulding in the three laboratories. As 50 loaves of each flour were baked by each formula and moulding procedure in the Manitoba laboratory, 25 were selected at random in order to simplify the statistical calculations required in comparing the data of the three laboratories. The number of loaves baked for each flour, formula, moulding method, and laboratory, together with the corresponding mean loaf volumes, are summarized in Table II. Additional statistical constants for Laboratories B and C are given in Table III; corresponding data for Laboratory A are given in Table XLI of the paper by Geddes *et al.* (1) which should be consulted for details regarding the statistical methods employed.

In all series, with the exception of flours Nos. 7 and 9 baked by the bromate formula in Laboratory C, machine moulding gave lower average loaf volumes than hand moulding, but the differences are not by any means constant. However, the mean responses to bromate of corresponding flours are in general of the same order of magnitude for the two methods of moulding.

In Laboratory A, machine moulding was found to effect a slight but significant reduction in the variability of replicate bakings. In Laboratory B, two flours, Nos. 7 and 9, baked by the bromate method, show significant differences in variability, one exhibiting greater and the other less variation by hand than by machine moulding. In Laboratory C, flours Nos. 6 and 9 baked by the simple formula are the only ones in which the differences in variability are significant and in both of these machine moulding had the advantage. The variabilities for all flours combined are not a satisfactory basis of comparison since these are influenced to a large extent by the variations in the general loaf volume levels of the different series of replicates included.

In order to determine whether machine moulding reduces the variability between replicates when the data for all flours and both baking formulas are considered and also to bring out other information, particularly the utility of mechanical moulding in reducing the differences between labor-

TABLE II
MEAN LOAF VOLUMES AND NUMBER OF LOAVES BAKED

Laboratory	Formula	No. 5		No. 6		No. 7		No. 8		No. 9		All flours	
		No.	Mean, cc.	No.	Mean, cc.	No.	Mean, cc.	No.	Mean, cc.	No.	Mean, cc.	No.	Mean, cc.
Hand moulding													
A	Simple	25	628.0	25	555.4	25	637.4	25	601.3	25	570.2	125	598.5
	Bromate	25	681.3	25	782.9	25	766.4	25	699.2	25	646.9	125	715.4
	Simple + bromate	50	654.6	50	669.2	50	701.9	50	650.3	50	608.6	250	656.9
B	Simple	25	496.8	25	551.4	25	610.8	25	539.8	25	513.6	125	562.5
	Bromate	25	648.0	24	731.9	25	739.8	25	696.0	25	624.6	124	687.7
	Simple + bromate	50	622.4	49	639.8	50	675.3	50	617.9	50	569.1	249	624.8
C	Simple	25	513.1	25	493.0	25	519.7	25	513.7	25	499.1	125	507.7
	Bromate	25	562.0	25	649.5	25	634.5	25	586.3	25	570.5	125	600.6
	Simple + bromate	50	537.5	50	571.2	50	577.1	50	550.0	50	534.8	250	554.1
A + B + C	Simple	75	579.3	75	533.3	75	589.3	75	551.6	75	527.6	375	556.2
	Bromate	75	630.4	74	721.3	75	713.6	75	660.5	75	614.0	374	667.8
	Simple + bromate	150	604.9	149	626.6	150	651.4	150	606.1	150	570.8	749	612.0
Machine moulding													
A	Simple	25	595.4	25	522.5	25	591.3	25	566.6	25	529.8	125	561.1
	Bromate	25	634.1	25	741.0	25	714.6	25	661.8	25	597.0	125	609.7
	Simple + bromate	50	614.7	50	631.8	50	652.9	50	614.2	50	563.4	250	615.4
B	Simple	25	574.8	25	532.4	25	561.4	25	516.2	25	484.0	125	533.8
	Bromate	25	621.0	24	683.5	25	701.2	25	669.4	25	592.6	124	653.3
	Simple + bromate	50	597.9	49	606.4	50	631.3	50	592.8	50	538.3	249	593.3
C	Simple	25	510.4	25	474.0	25	499.4	25	458.4	25	476.0	125	483.6
	Bromate	25	552.3	25	624.5	25	650.3	25	563.2	25	575.6	125	593.2
	Simple + bromate	50	531.4	50	549.2	50	574.8	50	510.8	50	525.8	250	538.4
A + B + C	Simple	75	560.2	75	509.6	75	550.7	75	513.7	75	496.6	375	526.2
	Bromate	75	602.5	74	681.9	75	688.7	75	631.4	75	588.4	374	638.7
	Simple + bromate	150	581.3	149	595.7	150	619.7	150	572.6	150	542.5	749	582.4

TABLE III
MACHINE *versus* HAND MOULDING BY EXPERIENCED OPERATORS IN DIFFERENT LABORATORIES
(Statistical constants pertaining to loaf volume data)

Flour No.	Baking formula	No. of loaves	Mean loaf volume				Diff. in L.V. by hand machine, cc.	Range in loaf volume		Standard deviation in L.V.		Sign of diff. in variability Z/σ	Coefficient of variability in L.V.	
			Hand moulded, cc.	Machine moulded, cc.	Response to bromate			Hand moulded, cc.	Machine moulded, cc.	Hand moulded, cc.	Machine moulded, cc.		Hand moulded, %	Machine moulded, %
					Hand	Machine								
Laboratory B														
5	Simple	25	596.8	574.8	51.2	46.2	22.0	50	60	13.03	13.38	0.13	2.18	2.33
5	Bromate	25	648.0	621.0			27.0	80	55	17.38	15.23	0.64	2.68	2.45
5	Simple	25	551.4	532.4	180.5	151.1	19.0	3.45	20	5.39	6.02	0.55	0.98	1.13
6	Bromate	25	731.9	683.5			48.4	40	60	12.06	16.68	1.56	1.65	2.44
6	Simple	25	610.8	561.4	129.0	139.8	49.4	8.09	50	11.72	10.73	0.43	1.92	1.91
7	Bromate	25	739.8	701.2			38.6	75	80	14.32	21.51	0.99	1.94	3.07
7	Simple	25	539.8	516.2	156.2	153.2	23.6	4.37	40	11.70	12.98	0.51	2.17	2.52
8	Bromate	25	696.0	669.4			26.6	3.82	70	16.00	7.79	3.53	2.30	1.16
8	Simple	25	513.6	484.0	111.0	108.6	29.6	5.76	80	26.40	18.38	1.77	5.14	3.80
9	Bromate	25	624.6	592.6			32.0	5.12	60	17.37	14.70	0.82	2.78	2.45
9	Simple	125	562.5	533.8	125.2	119.5	28.7	5.10	155	39.28	34.85	1.33	6.98	6.53
Entire series	Bromate	124	687.7	653.3			34.4	5.00	190	47.98	43.53	1.08	6.98	6.66
	Simple + bromate	249	624.8	593.3			31.5	5.04	300	76.42	71.60	1.02	12.23	12.07
Laboratory C														
5	Simple	25	513.1	510.4	48.9	41.9	2.7	100	63	21.08	16.96	1.07	4.11	3.32
5	Bromate	25	562.0	552.3			9.7	1.73	58	17.51	17.51	0.38	2.88	3.17
5	Simple	25	493.0	474.0	156.5	150.5	19.0	3.85	58	12.68	8.49	1.96	2.57	1.79
6	Bromate	25	649.5	624.5			25.0	3.91	131	28.84	34.13	0.82	4.44	5.46
6	Simple	25	519.7	499.4	114.8	150.9	20.3	3.91	57	15.26	12.07	1.15	2.42	2.42
7	Bromate	25	634.5	650.3			15.8	2.49	90	24.61	26.43	0.35	3.88	4.06
7	Simple	25	513.7	458.4	72.6	104.8	55.3	10.76	106	19.32	20.88	0.38	3.76	4.56
8	Bromate	25	586.3	563.2			23.1	3.94	50	13.73	14.29	0.20	2.34	2.54
8	Simple	25	499.1	476.0	71.4	99.6	23.1	4.63	89	21.45	11.72	2.96	3.36	2.46
9	Bromate	25	570.5	575.6			5.1	8.94	85	19.19	27.12	1.69	3.36	4.71
9	Simple	125	507.7	483.6	92.9	109.6	24.1	4.75	128	20.84	23.81	1.48	4.10	4.63
Entire series	Bromate	125	600.6	593.2			7.4	1.23	214	40.99	45.24	1.10	6.82	7.62
	Simple + bromate	250	554.1	538.4			15.7	2.83	286	56.68	65.64	2.31	10.23	12.19

atories, the analyses of variance summarized in Table IV were made. The standard errors given at the foot of the table were computed from the corresponding error variances (differences between replicates) given in the variance analysis tables. The standard errors of single determinations are in reality pooled standard deviations for the differences between replicates and they have been compared by means of the *Z* test. While the random errors for machine moulding are significantly lower than for hand moulding in the instance of Laboratory A, there is no significant difference for Laboratories B and C or for all laboratories combined. The random errors for the different laboratories by each moulding procedure may also be compared by the *Z* test. Laboratory C has a significantly higher error for both hand and machine moulding than Laboratory B, and is also significantly higher than Laboratory A in the instance of machine moulding. It must, therefore, be concluded that the higher experimental error for this laboratory is due to factors other than moulding technique.

The *Z* values for "differences between flours" measure the significance of the differences between the mean loaf volumes (simple and bromate formulas combined) of the various flours. The corresponding *Z* values for hand and machine moulding are very similar, indicating that there is no essential difference between the two moulding procedures in their utility in differentiating between flours. For example, from Table II it will be noted that, by both procedures and in all laboratories, Flour 9 gave the lowest mean volume and Flour 7 the highest. The ranges of the means for flours for Laboratory A are 93.3 cc. and 89.5 cc. for hand and machine moulding respectively, for Laboratory B 106.2 and 93.0 cc., for Laboratory C 42.3 and 49.0 cc. and for all laboratories combined, 80.6 cc. and 77.2 cc.

The *Z* values for the "differences between formulas" are, in general, also of the same order of magnitude for hand and machine moulding. In Laboratory A the range between the simple and bromate formula is 116.9 cc. and 108.6 cc. for hand and machine moulding respectively, for Laboratory B 125.3 and 119.5 cc., for Laboratory C 93.1 and 109.6 cc., and for the three laboratories combined 111.6 and 112.5 cc.

Similarly, the *Z* values for interaction "flours \times baking formulas" correspond quite closely for the two methods of moulding, and it may be concluded that from the standpoints of differentiating between flours, measuring the response to bromate and the differential behavior of flours to this oxidizing agent, machine moulding gives essentially the same information as hand moulding.

The *Z* values for the differences between laboratories are of particular interest. For hand moulding $Z = 3.7126$ and for machine moulding 3.4587, thus indicating that machine moulding tends to reduce slightly the variability between laboratories. Thus, from Table II it will be noted that the mean loaf volumes for Laboratories A, B and C are 657, 625 and 554 cc. respectively, for hand moulding, while the corresponding values for machine moulding are 615, 593 and 538 cc. The ranges in the mean volumes for the three laboratories are 103 cc. for hand and 77 cc. for machine moulding.

TABLE IV
MACHINE VERSUS HAND MOULDING BY EXPERIENCED OPERATORS
(Analysis of variance for loaf volume data)

Variance due to	Degrees of freedom	Variance		Z		5% point
		Hand moulding	Machine moulding	Hand moulding	Machine moulding	
Laboratory A						
Differences between flours	4	57,063.6	54,759.6	2.5451	2.8007	0.4397
Differences between baking formulas	1	854,042.1	736,905.4	3.8980	4.0764	0.6780
Interaction, flours \times formulas	4	57,457.4	59,653.1	2.5485	2.8194	0.4397
Differences between replicates	240	351.3	212.2			
Laboratory B						
Differences between flours	4	74,080.6	58,241.5	2.8489	2.7961	0.4397
Differences between baking formulas	1	976,092.4	889,622.4	4.1381	4.1592	0.6780
Interaction, flours \times formulas	4	30,628.5	25,470.3	2.4072	2.3825	0.4397
Differences between replicates	239	248.4	217.1			
Laboratory C						
Differences between flours	4	18,578.8	30,219.6	1.9079	2.1190	0.4397
Differences between baking formulas	1	538,982.6	750,431.2	3.5918	3.7250	0.6780
Interaction, flours \times formulas	4	22,945.6	25,286.3	2.0135	2.0298	0.4397
Differences between replicates	240	409.1	436.3			
Laboratories A, B and C Combined						
Differences between flours	4	133,173.8	122,156.2	2.8892	2.8744	0.4345
Differences between laboratories	2	691,278.8	392,974.4	3.7126	3.4587	0.5507
Differences between baking formulas	1	2,332,427.1	2,371,136.0	4.3207	4.3573	0.6746
Interactions,						
Flours \times laboratories	8	8,274.6	10,532.3	1.4999	1.6490	0.3341
Flours \times baking formulas	4	96,606.2	91,722.6	2.7287	2.7312	0.4345
Laboratories \times baking formulas	2	18,345.0	2,911.5	1.8981	1.0061	0.5507
Differences between replicates	727	412.0	389.2			
Standard Errors						
Laboratory	Hand, cc.	Machine, cc.	Significance of difference, Hand vs. machine			
			Z		5% point	
A	18.74	14.57	0.2522		0.1064	
B	15.76	14.73	0.0675		0.1064	
C	20.23	20.89	0.0322		0.1064	
A, B and C	20.30	19.73	0.0284		0.0610	

The variation among the three laboratories is very wide, and since machine moulding only reduced the difference by approximately one-third, the lower loaf volumes of Laboratory C must be due largely to factors other than moulding technique.

The significant interaction "flours \times laboratories" is of importance since it implies that the different laboratories did not obtain the same relative results with the various flours. This interaction is based on the mean loaf

TABLE V
INTERACTION TABLE FOR "FLOURS \times LABORATORIES"
MEAN LOAF VOLUMES
(Combined results for simple and bromate formulas and
for hand and machine moulding)

Flour No.	Laboratory			
	A, cc.	B, cc.	C, cc.	A+B+C, cc.
9	586	554	530	557
8	632	605	530	589
5	635	610	534	593
6	650	623	560	611
7	677	653	576	636
All flours	636	609	546	597

volumes of each flour for both baking formulas and moulding procedures. These are recorded in Table V, the flours being arranged in order of increasing loaf volume as determined in Laboratory A. The order in which the flours are placed is almost identical for the three laboratories, the interaction being chiefly due to the similarity in the mean volumes of flours Nos. 9, 8 and 5 in Laboratory C.

A statistical summary of the data obtained by the different bakers in Laboratories B and C is given in Table VI. In Laboratory B all the bakers were trained technicians, whereas in Laboratory C, bakers A and B were both experienced but the latter only baked at irregular intervals; baker C was the experimental miller and had no previous baking experience whatever.

Considering first the results obtained in Laboratory B, bakers A and B secured higher variability between replicates for machine moulding although the differences are not significant. The pooled standard deviation for the three technicians, calculated from the error variance, is 16.8 cc. and 19.8 cc. for hand and machine moulding respectively. Since the Z value for the difference is 0.1640 with a 5% point of 0.1933, the higher variability for machine moulding is not statistically significant. The range in mean loaf volume for the three bakers is 7.4 cc. and 18.8 cc. for hand and machine moulding respectively. Since the corresponding Z values for the "differences between bakers" are 0.1592 and 0.8858 with 5% points of 0.5696, the differences in mean loaf volume obtained by the three bakers are significant for machine but not for hand moulding.

The results in Laboratory B appear to warrant the conclusion that experienced bakers trained in one laboratory are likely to produce more consistent results by hand than by machine moulding. The use of a mechanical moulder, would, however, be justified, if through its use more consistent results could

TABLE VI
HAND VERSUS MACHINE MOULDING BY DIFFERENT BAKERS
(Statistical constants for loaf volume data)

		Baker			All bakers
		A	B	C	
<i>Laboratory B—Flour No. 7 baked by bromate formula</i>					
Number of replicates,	Hand	25	25	25	75
	Machine	25	25	25	75
Mean, cc.,	Hand	739.8	747.2	741.2	742.7
	Machine	701.2	707.4	688.6	699.1
Mean difference (Hand — machine), cc.		38.6	39.8	52.6	43.6
Standard deviation (σ) cc.,	Hand	14.61	16.65	18.78	16.85
	Machine	21.95	20.87	15.91	21.02
Significance of difference in S.D., Z/σ_z		1.41	0.78	0.57	1.90
Coefficient of variability (C.V.), %,	Hand	1.98	2.23	2.53	2.27
	Machine	3.13	2.95	2.31	3.01

Analyses of variance

Variance due to	Degrees of freedom	Variance		Z		5% point
		Hand	Machine	Hand	Machine	
Difference between bakers	2	386.50	2,294.50	0.1592	0.8858	0.5696
Difference between replicates	72	281.13	390.22			
Standard error of 1 determination		16.77	19.75			
Standard error of means for bakers		3.35	3.95			

		Baker			All bakers
		A	B	C	
<i>Laboratory C—Flour No. 5 baked by bromate formula</i>					
Number of replicates	Hand	25	24	25	74
	Machine	25	24	25	74
Mean, cc.,	Hand	562.0	591.6	515.5	555.9
	Machine	552.3	597.4	547.9	565.4
Mean difference (Hand — machine), cc.		9.7	—5.8	—32.4	—9.5
Standard deviation (σ) cc.,	Hand	16.52	19.98	18.59	36.33
	Machine	17.87	21.57	15.43	28.90
Significance of difference in S.D., Z/σ_z		0.27	0.27	0.65	2.00
Coefficient of variability (C.V.), %	Hand	2.94	3.38	3.61	6.54
	Machine	3.24	3.61	2.82	5.11

TABLE VI—*Concluded*
 HAND *versus* MACHINE MOULDING BY DIFFERENT BAKERS—*Concluded*
 (Statistical constants for loaf volume data)

Variance due to	Degrees of freedom	Variance		Z		5% point
		Hand	Machine	Hand	Machine	
Analyses of variance						
Difference between bakers	2	36,162.24	18,226.70	2.3359	1.9920	0.5699
Differences between replicates	71	338.34	339.20			
Standard error of 1 determination		18.39	18.42			
Standard error of means for bakers		3.68	3.68			

be secured by inexperienced technicians. The data obtained in Laboratory C are of interest in this connection since baker C had no baking experience whatever and baker B was out of practice. The two experienced bakers secured slightly lower variability between replicates by hand moulding while machine moulding gave the lowest variability for baker C. In no instance, however, are the differences significant and the pooled error variances for hand and machine moulding are practically identical. It is interesting to note that in hand moulding, the relative variability (coefficient of variation) for the three bakers tends to vary inversely as their baking experience, a trend which is in line with previous observations in this connection.

Considering the mean loaf volumes, bakers B and C secured higher volumes by machine than by hand moulding, with the result that the spread between the bakers is reduced from 86 cc. for hand moulding to 46.5 cc. for machine moulding. However the variance for the "differences between bakers" is still highly significant and factors in addition to moulding technique must therefore materially contribute to the low mean loaf volumes obtained by the inexperienced operator. Geddes *et al.* (1) have previously shown that inexperienced operators tend to secure lower loaf volumes and higher relative variabilities than experienced bakers and that the manual operations involved in both punching and moulding contribute to the differences between bakers.

Discussion

These studies show quite clearly that differences in the manual manipulation of doughs during moulding are relatively unimportant in relation to the total effect of other factors causing variability between replicates. While mechanical moulding reduced, to some extent, the variability between experienced bakers working in different laboratories, the differences were still very great and the bakers fell in the same order in regard to mean loaf volume for both hand and machine moulding, indicating that some systematic factors were operating which affected similarly both the hand and machine

results. That factors other than moulding contribute greatly to the variability between bakers is also indicated by the similar order of the mean loaf volumes for hand and machine moulding obtained by the three experienced bakers in Laboratory B; in this instance the variability between operators was greater for machine moulding. The data secured in Laboratory C by operators of varying experience indicate that mechanical moulding enables an inexperienced baker to secure mean volumes more closely approaching those obtained by trained technicians.

The present study supplements and, in general, confirms the results reported by Geddes *et al.* (1) who found that the personal element, both in punching and moulding, contributed to the variability between bakers and, accordingly, stated that mechanical moulding alone could not be expected to eliminate the large differences in mean loaf volume which different operators secure in replicate bakings of the same flour.

Acknowledgments

The Associate Committee on Grain Research is indebted to the Thomson Machine Company, Belleville, New Jersey, for their kindness in lending the mechanical moulder.

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CAMBIAL ACTIVITY IN POPLAR WITH PARTICULAR REFERENCE TO POLARITY PHENOMENA¹

BY A. B. BROWN²

Abstract

Ring-boring experiments with the aspen poplar, *Populus tremuloides* Michx., lead to the conclusion that cambial activity is definitely not rigidly or unconditionally polar in its development in the root. A much greater development of cambial activity in the morphologically upward direction was obtained in these experiments than has hitherto been observed. It is suggested that the concept of polarity, applied to cambial activity as a process, must be defined in terms of a tendency to develop in the morphologically downward direction, rather than in the morphologically upward direction, in roots and stems. Polarity in relation to cambial activity in general is discussed briefly.

Introduction

In a previous communication, the writer (1) showed that cambial activity, emanating from sucker shoots of poplar, flows apparently almost entirely in the distal direction on entering the parent root, resulting in marked thickening of the root on the distal side, except in cases where sucker shoots occur very close to one another, when this distal thickening may not be obvious. This type of behavior is expressed invariably however, in the grain of the wood, which runs longitudinally down the sucker shoot and continues likewise along the root in the distal or acropetal direction. In the crotch, *i.e.*, the region common to both shoot and root, the grain runs longitudinally at all points on the distal side, but on the proximal side it divides, turns sharply through an angle of 90°, and then swings round to run longitudinally and distally. As a result, in longitudinal radial sections of the root and sucker shoot at the crotch, the xylem elements are cut longitudinally on the distal side, whereas on the proximal side, in the region common to both root and shoot, the xylem elements are cut more or less transversely. It was also shown that the tissue orientations just described are anticipated at a very early stage; *viz.*, around the base of the sucker bud from which the sucker shoot ultimately develops. Vascular connection between the sucker bud and the root xylem is attained by the development of a peg of tracheids. As a result of the interaction between the normal acropetal flow of cambial activity in the root and this vascular peg, the tissues subsequently formed turn sharply on the proximal side and orient themselves around the peg, as seen in longitudinal tangential sections, in a form essentially similar to that of a flow-pattern. In longitudinal radial section, the root xylem is cut transversely just proximal to the vascular peg and longitudinally on the distal side.

In the early part of the summer, soon after the basipetal flow of cambial activity from the shoot has reached the root, a well defined gradient of cambial activity, estimated in terms of xylem formation, can be detected, running from the base of the shoot, along the root in the distal direction. At the same time however, a feeble gradient in the opposite direction can be observed,

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running from the base of the shoot, along the root in the proximal direction. Certain investigators, who will be referred to later, postulate that cambial activity is polar, in so far as it can only travel in the morphologically downward direction in the stem, and in the acropetal direction in the root. However, in view of the gradient of xylem formation in the *proximal* direction, feeble though it may be, it would appear that polarity of cambial activity is not complete and unconditional. It was thought worth while therefore, to investigate further the polarity of cambial development in this material, and the following experiments were designed expressly to yield some information on this subject. The fact that cambial activity is evidently not completely polar in development suggested to the writer (1) the possibility that the flow of cambial activity from the shoot may actually be guided along the root in the distal direction, as a result of the re-orientation of the tissues around the vascular peg at the base of the sucker bud from which the shoot arises. In other words, the phenomenon could conceivably be explained, in a very simple manner, without postulating polarity. On the other hand, it should be remembered that there are a number of phenomena indicative of polarity of cambial activity that could not be so explained.

Experiments and Results

PART 1. EXTENT OF DEVELOPMENT OF CAMBIAL ACTIVITY IN THE PROXIMAL DIRECTION IN ROOTS UNDER EXPERIMENTAL CONDITIONS

The material used was aspen poplar, *Populus tremuloides* Michx., and three different experiments, A, B and C (Fig. 1), were performed. In Experiment A the root was completely ringed some distance proximal to the sucker shoot,

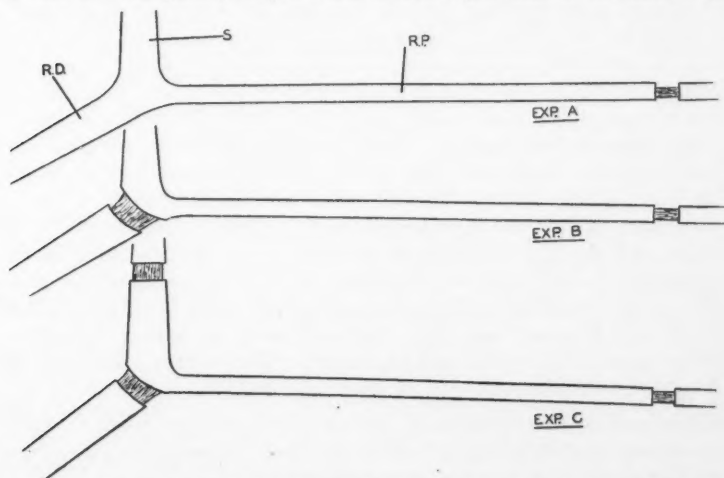


FIG. 1. Illustrating the relative positions of the complete rings in Experiments A, B and C. S = the sucker shoot, R.D. = the root distal to the shoot, and R.P. = the root proximal to the shoot.

in such a way as to remove all the tissues external to the xylem. In Experiment B, two complete rings were made, one proximal to the sucker shoot just as in Experiment A, and one immediately distal to the sucker shoot. In Experiment C three rings were made, one some distance proximal to the sucker, one immediately distal, and the third a short distance up the shoot. All growing points, if any, below the stem ring were removed. It was found that unless the ring was made quite close to the base of the stem, death of the parts above the ring ensued comparatively soon, whereas when the stem ring was near the base, the parts above could remain alive until the end of the growing season. In these experiments, the distance between the crotch and the proximal ring varied from 6 to 40 inches and was determined simply by the habit of the material. The sucker shoots varied in age from 5 to 14 years, and the operations were carried out within the last two weeks in May and the first week in June, in the years 1934 and 1935. At that time new xylem formation had not commenced in the roots. In all, about 100 trees were treated. The roots were uncovered as carefully as possible, and the operations performed on the trees as they occurred *in situ*. The exposed xylem in the rings was thoroughly scraped with a scalpel and the wound then rubbed with vaseline and finally covered with grafting wax. No healing over of the wounds ever took place. Usually the exposed roots were covered with loose turf after the operation. There was a marked tendency for sucker buds to arise just distal to the rings in the root, particularly the ring proximal to the sucker shoot. This tendency was not so evident just distal to the ring immediately distal to the shoot. These buds were usually removed whenever they were detected.

Subsequent growth of the treated trees was quite normal in the case of Experiment A. In B- and C-treated plants, the leaves tended to be smaller than usual and took on a bronze coloration at an early date. However, it was not at all uncommon to find trees receiving the B treatment perfectly normal in appearance with regard to leaf size and color. No difference in time was observed with respect to leaf fall at the end of the season. A few A- and B-treated specimens were left to overwinter and in the following spring they all leafed out at the same time as untreated trees. In most of the A-treated trees which had overwintered, the root proximal to the sucker was found to have died, either during the winter or early in the second season. Otherwise, the A-treated trees were perfectly normal during the second season. In B material the leaves were smaller, and bronzed early in all the specimens that had overwintered, and there appeared to be a definite reduction in extension growth during the second season. The specimens were still alive on August 9, 1935, when all of them were collected.

With regard to cambial activity, estimated in terms of xylem formation, the results can be summed up as follows: A falling gradient of xylem formation in the root on the side *proximal* to the sucker shoot was obtained in all three experiments. It was least marked in C material and most marked in B, while A was intermediate. The following estimations of the width of the

annual ring at different distances from the sucker shoot in four experiments, A 14(24 in.), A 16(16 in.), B 3(14 in.) and B 13(37 in.) (Tables I and II), will indicate the type of xylem gradient obtained in Experiments A and B. The figure in brackets after the number of the experiment indicates the length between the shoot-root crotch and the ring proximal to the crotch. All widths are compared with the width of the annual-growth ring for the current year in the shoot at a distance of six inches from its base, and this is arbitrarily rated at 100 in all cases. In no experiment were there any growing points on the shoot lower than six inches from its base. The actual widths of the annual ring in the shoot, six inches from the base, in A 16, A 14, B 3 and B 13, were, in arbitrary units, 140, 40, 32 and 37 respectively. It will be observed that there was very little difference between the widths in A 14, B 3 and B 13, so that the figures for these three experiments can be compared with one another in terms of actual width without any great error.

It is clear from the above results that a very appreciable gradient of cambial activity was laid down in the root *proximal* to the sucker shoot, in a system otherwise untreated except for a complete ring some distance proximal to the shoot (Experiments A 16 and A 14). There was no question of any stimulus passing across the ring, for precisely the same result obtained if the root was cut through completely, instead of ringed. Apparently, there-

TABLE I
EXPERIMENTS A 16 AND A 14

	Width of annual ring	
	A 16	A 14
Stem: 6 in. from base	100	100
Root: 1 in. distal to shoot	150	136
Root: 6 in. distal to shoot	150	69
Root: 1 in. proximal to shoot	63	36
Root: 3 in. proximal to shoot	49	29
Root: 6 in. proximal to shoot	38	26
Root: 9 in. proximal to shoot	30	22
Root: 12 in. proximal to shoot	25	19
Root: 15 in. proximal to shoot	15	16
Root: 18 in. proximal to shoot		13
Root: 21 in. proximal to shoot		10
Treated	3/6/35	3/6/35
Collected	9/8/35	4/9/35

TABLE II
EXPERIMENTS B 3 AND B 13

	Width of annual ring	
	B 3	B 13
Stem: 6 in. from base.....	100	100
Root: 1 in. proximal to shoot	150	324
Root: 3 in. proximal to shoot	103	216
Root: 6 in. proximal to shoot	75	108
Root: 9 in. proximal to shoot	58	117
Root: 12 in. proximal to shoot	50	102
Root: 15 in. proximal to shoot		95
Root: 18 in. proximal to shoot		95
Root: 21 in. proximal to shoot		102
Root: 24 in. proximal to shoot		102
Root: 27 in. proximal to shoot		87
Root: 30 in. proximal to shoot		70
Root: 33 in. proximal to shoot		50
Root: 35 in. proximal to shoot		27
Treated	29/5/35	3/6/35
Collected	9/8/35	9/8/35

fore, cambial activity is not rigidly polar in its development in the root. In Experiment B the gradient of xylem, laid down in the root on the proximal side, was not less and usually greater than that found on the distal side in untreated, or A-treated material. On the whole, it was found that the gradient on the proximal side in B material fell off rather more rapidly than it did on the distal side in A material. There was no indication whatsoever of any re-orientation of the tissues in the shoot-root crotch, despite the fact that the distal ring was shaped (Fig. 1), with the aim in view of facilitating any changes that might tend to take place.

Now it is well known that a basifugal development of cambial activity takes place locally from the upper edge of a complete ring in a shoot, quite independent of developing buds or elongation growth. Precisely the same sort of behavior occurs in roots, and Experiment C yielded information on this point. It will suffice to state that the gradient of xylem formation obtained in the proximal direction was exceedingly feeble. Several rows of xylem elements might be laid down just proximal to the shoot, but at a very short distance proximal, about 4 inches, the gradient practically faded out. The amount of xylem laid down proximal to the shoot in B material was, without a doubt, much greater than could be accounted for, if it were compounded simply of the amount of xylem formed as a result of A treatment plus the development resulting from C treatment.

A word now about the anatomical features of the new xylem laid down proximally in the root in these experiments. Almost invariably in Experiments A and B, the xylem in the root was denser than that of previous years. This was due principally to the fact that the vessels were smaller. Indeed, the new wood rather resembled typical stem wood. Occasionally a little parenchyma was found, formed at the beginning of cambial activity, but the new wood was not at all characterized by the presence of parenchyma as a constant feature, except towards the end of the gradient where it approached the ring proximal to the shoot. Here the wood invariably did include an abundance of parenchyma. Otherwise the wood laid down proximally was quite normal, consisting of vessels, tracheids, fibres and medullary rays. In Experiment C the new xylem did appear to be rather atypical. The conducting elements were again smaller in diameter, they often occurred in groups and consisted chiefly of tracheids rather than vessels, which although present were rather scarce. Moreover, the fibres were not thickened to nearly the same extent as in Experiments A and B. The wood laid down immediately distal to the shoot in normal untreated roots is usually rather denser and more like stem wood than that found at points further removed from the shoot, but it was observed in Experiment A, that the current year's wood distal to the shoot was not infrequently denser than that laid down in previous years. Moreover, one occasionally did find cases of A and B experiments, where the wood formed in the root proximal to the shoot was not markedly denser than the previously formed wood, particularly beyond the immediate vicinity of the shoot. It is quite possible that the formation of

denser wood in the roots in these experiments was determined to a certain extent by some such factor as water supply. Many of the feeder roots were inevitably destroyed during excavation prior to operation, and normal translocation of water would very probably be upset as a result of ringing, particularly in Experiments B and C. The wood laid down in the shoot in Experiments A and B was quite typical and did not appear to differ at all from that of previous years. A point of considerable interest is that the width of the post-operative growth ring in the shoot was sometimes greater and sometimes less than that of the previous year in both A and B experiments. In B material however, there was a marked decrease in width of the growth ring in the second season after operation, *i.e.*, in trees that had overwintered.

In Fig. 4; A, B and C illustrate the type of development obtained in three experiments, A1, B23 and C1. They show clearly that the wood formed in the root proximal to the shoot after the operative procedure is markedly denser than that of previous years. Moreover they give some idea of the extent of development that can be obtained in Experiments A and B at a considerable distance, seven inches, proximal to the shoot-root crotch. In C1 the section illustrated was cut at slightly less than one inch from the crotch; at a distance of seven inches from the crotch no new xylem had been formed. It was found, in all the B experiments, that for at least a considerable distance proximal to the shoot, the current year's growth ring was wider than any other growth ring laid down in that region previous to the operation. This applied only to the first post-operative growth ring. As has already been pointed out, development in the second season after operation was rather feeble. In Experiment A1 (Fig. 4, A), the current year's growth ring is wider than any of the others shown, but not as wide as some of the rings nearer the centre of the section and not included in the photograph. The only generalization that can be made with regard to the A experiments is that the width of the growth ring formed after the operation was not always less than that of previously formed rings. As far as the writer is aware, cambial activity in the proximal or morphologically upward direction has not hitherto been observed to the extent obtained in either Experiment A or B, with roots of poplar.

PART 2. TISSUE ORIENTATIONS IN RELATION TO A WOUND WHEN CAMBIAL DEVELOPMENT IS PROXIMAL IN THE ROOT

In a woody stem, if instead of making a complete ring a longitudinal phloem bridge is left, it is found that cambial activity accumulates or "piles up" immediately above or distal to the wound, flows through the bridge and then spreads out downwards and obliquely round the stem below the wound (Fig. 2). Transverse sections just above the wound show the xylem to be cut transversely at all points, except where the elements turn in slightly towards the bridge where they may be cut very slightly obliquely, whereas just below the wound the xylem is cut transversely only in the same longitudinal line as the bridge, and definitely obliquely at all other points. It is not proposed to discuss this type of behavior in any detail in this paper; what is of particular

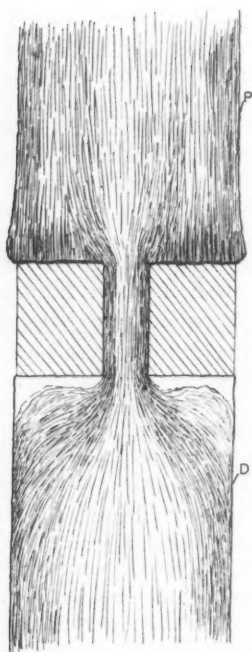


FIG. 2. Tissue orientations in the wood of a shoot or root in relation to a ring with a longitudinal phloem bridge remaining. P = the root proximal to the wound or the shoot above the wound, D = the root distal to the wound or the shoot below the wound.

inches from the crotch and the phloem bridge was somewhat less than one inch long. Note that the point seven inches proximal to the shoot was really distal to the wound, and the point eight inches proximal to the shoot really proximal to the wound, in terms of location on the root.

It is clear from the above analysis that wounding has

interest is that it may be considered to be a typically polar phenomenon. Precisely the same type of behavior obtains in similarly wounded roots. The accumulation or "piling up" of xylem formation occurs on the proximal side of the wound, and the spreading out on the distal side. Wounds of this type were accordingly made in Experiments A and B, in that region of the root between the sucker shoot and the proximal complete ring, at a time when the cambium was still active and after a considerable gradient of xylem formation had been laid down in the proximal direction. *In every case the orientation of the tissues subsequently formed in relation to the wound was absolutely normal. There was no reversal either in Experiments A or B.* The following analysis of Experiment A 5 illustrates the type of result obtained. There were two dates of treatment, the first when the complete ring proximal to the shoot was made, and the second when the wound with the longitudinal phloem bridge was made. The second wound was located at about seven

TABLE III
EXPERIMENT A 5

(1st treatment, 12/5/34) (2nd treatment, 3/7/34)
(Collected, 23/7/34)

	Width of annual ring
Stem: 3 in. from base	100
Root: 2 in. distal to shoot	112
Root: 6 in. distal to shoot	93
Root: 1 in. proximal to shoot	39
Root: 2 in. proximal to shoot	35
Root: 3 in. proximal to shoot	32
Root: 4 in. proximal to shoot	31 + 0 to 7
Root: 5 in. proximal to shoot	27 + 7 to 14
Root: 6 in. proximal to shoot	24 + 14 to 17
Root: 7 in. proximal to shoot	23 + 1 to 27*
Root: 7.5 in. proximal to shoot	21 + 37†
Root: 8 in. proximal to shoot	21 + 20 to 27**
Root: 9 in. proximal to shoot	19 + 13
Root: 10 in. proximal to shoot	27 (= 18 + 9)
Root: 11 in. proximal to shoot	19 (= 16 + 3)
Root: 12 in. proximal to shoot	15

*Immediately distal to bridge.

†Within bridge.

**Immediately proximal to bridge.

brought about a marked increase in cambial activity in the vicinity of the wound. Moreover, the first xylem formed after wounding consisted largely of vessels, so that what was really a false growth-ring developed, enabling one to measure the extent of development prior to and subsequent to wounding. A few inches proximal to the wound, the demarcation between the wood formed prior to wounding and that formed after was not clear (this seems to be a constant feature), and the figures in brackets at 10 and 11 inches proximal to the shoot are rough extrapolations. As has already been stated, the tissue orientations around the wound were quite normal, no reversal having taken place. This is clearly indicated in the figures. Just proximal to the phloem bridge, the new wood laid down after wounding was but slightly excentric (20-27) and the elements were all cut transversely, whereas the new wood just distal to the bridge was very markedly excentric (1-27) and was cut transversely only in the same longitudinal line as the bridge, and obliquely at all other points as it spread downwards and obliquely round the root. The width of the new wood laid down in the bridge itself subsequent to wounding was always greater than that immediately distal or proximal to the wound. This was a constant feature. Precisely the same results were obtained in the B experiments. Fig. 4, D depicts a transverse section of the root within the bridge in Experiment B 2, and shows the extent of development prior to and subsequent to wounding at the time of collection. The results were definite and absolutely invariable, even when the wound was little more than one inch from the crotch. Moreover, the same result was obtained in four B experiments, with trees that had overwintered and were in their second season of growth after the first operative treatment. Here again, there was no reversal of the orientation of the tissues around the wound with the longitudinal phloem bridge. Whether similar results would be obtained in the third season of growth is not known. B material did rather poorly in its second season. There was less extension growth, fewer leaves produced, and a marked decrease in the amount of cambial activity. No experiments were performed with A material in the second season. Of the few that were left to overwinter, in most cases the root proximal to the sucker had died or was otherwise unsuitable for further treatment. The wood formed subsequent to wounding in these experiments was apparently quite normal. In Experiment B 2 (Fig. 4, D), the wood formed after wounding was somewhat denser than that laid down before wounding, but this was not always the case.

The complication arising from the above results is probably obvious. It is simply this, that there was no reversal of the tissue orientations around the wound with the longitudinal phloem bridge, under conditions where such a reversal might reasonably have been expected. The development of cambial activity is normally basipetal in the shoot and acropetal in the root, and the orientation of the tissues with relation to a wound with a longitudinal phloem bridge, in an otherwise untreated shoot or root (Fig. 2), could very naturally be interpreted as simply a manifestation of the normal mode of development.

From this point of view therefore, the fact that there was no reversal in Experiments A and B is rather surprising. There is however at least one point that may be of considerable significance in this connection. If a wound of the type under consideration is made in a dormant shoot or root, cambial activity is initiated locally around the wound, quite independent of cambial activity emanating from developing buds, which may indeed be entirely removed. Moreover, the new tissues orientate themselves in the vicinity of the wound precisely in the manner described above. Apparently to get cambial activity as a result of wounding, the phloem must be cut in such a way as to cause discontinuity of the elements. Any transverse or oblique incision would bring this about, whereas a longitudinal incision possibly would not if the elements were running strictly longitudinally. In addition, cambial activity only occurs if the cut has phloem tissue immediately distal to it in the stem, or proximal to it in the case of the root. This is clearly expressed in the fact that, if a complete ring is made in a stem, cambial activity leads to the production of a *basifugal* gradient of xylem from the upper margin of the ring, whereas no cambial activity is evident at the lower margin. It is, therefore, not inconceivable that the orientation of the tissues superimposed upon the proximal gradient in Experiments A and B was governed by the phloem tissue formed before the first operative procedure, despite the fact that a certain amount of new phloem had also been laid down, presumably in the same manner as the xylem, in a proximal gradient. But on the other hand, there was no evidence that the *amount* of cambial activity, superimposed upon the proximal gradient in the vicinity of the wound with the longitudinal phloem bridge, was determined by the phloem formed previous to the first operative procedure, since it was always greater relative to the amount of cambial activity obtained in the C experiments.

PART 3. RELATIONSHIP BETWEEN CAMBIAL ACTIVITY AND GROWTH OF SUCKER BUDS, IN REGIONS OF THE ROOT WHERE THE NORMAL DISTAL DEVELOPMENT OF CAMBIAL ACTIVITY IS NOT TAKING PLACE

During the course of the above experiments, the writer was able to make observations of marked significance with relation to the behavior of sucker buds, which, if they did not arise definitely after, at least had not made vascular connection with the root xylem prior to, the operative procedure. These observations apply to such buds arising distal to the distal complete ring in Experiment B, or between two complete rings in regions of the root having no phloem connection with sucker shoots, as in Experiment C, and making vascular connection with the parent root in regions where the cambium was not dividing and the normal acropetal flow of cambial activity not present. Fig. 3 illustrates the manner in which the new xylem resulting from bud activity is laid down upon the surface of the wood of the previous year, as observed in pieces of root which had been peeled and allowed to dry out. Generally speaking, the new wood runs acropetally downwards and obliquely round the surface of the old wood. But just proximal to the bud, the new

wood actually runs almost directly proximal for a short distance before it turns. The writer has already pointed out that sucker buds tended to arise just distal to a complete ring, but wishes to emphasize that the behavior illustrated was commonly observed at points considerably removed from any complete ring. Behavior of similar buds close to a complete ring was, however, the same. Precisely the same type of behavior was observed close to the complete ring proximal to the shoot in Experiments A and B, again with buds that had not attained vascular connection with the root prior to operation. Here, surprisingly enough, the wood resulting from bud activity spread distally or acropetally upon the surface of wood that had been, or was being laid down in a gradient in the opposite or proximal direction. It is true, however, that these buds were always observed very close to the complete ring, *i.e.*, right at the end of the proximal gradient where the xylem contained an abundance of parenchyma.

A point of interest arising at this time is related to a former statement by the writer (1), to the effect, that the definite "flow pattern" in the root xylem below the sucker bud under normal conditions is a manifestation of the reaction between root cambial activity and the obstruction offered by the vascular peg at the base of the sucker bud. In view of the above observations, bud activity of itself could not bring about the formation of such a pattern, and so the writer's earlier statement receives some support.

PART 4. SIMILAR EXPERIMENTS WITH POPLAR STEMS

The reader will probably be able, without much difficulty, to picture experiments with stems, essentially similar to those already described with roots. Instead of the shoot-root crotch we have now to consider the branch crotch. Corresponding to Experiment A, one complete ring was made in one member of the crotch and this limb was completely disbudded below the ring. The other limb was untreated. Corresponding to Experiment B, a second complete ring was made immediately below the crotch, and corresponding to Experiment C, three complete rings were made, one on each of the two limbs and another immediately below the crotch. The material between the rings was completely disbudded. Ringing was carried out during the month of April, before the advent of bud break. The results will be

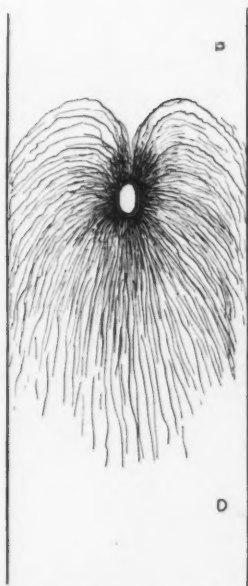


FIG. 3. Illustrating the way in which cambial activity emanating from developing buds spreads over the surface of the previously formed wood, in regions of the root where the normal acropetal flow of cambial activity is not present. P = the root proximal to the bud, D = the root distal to the bud.

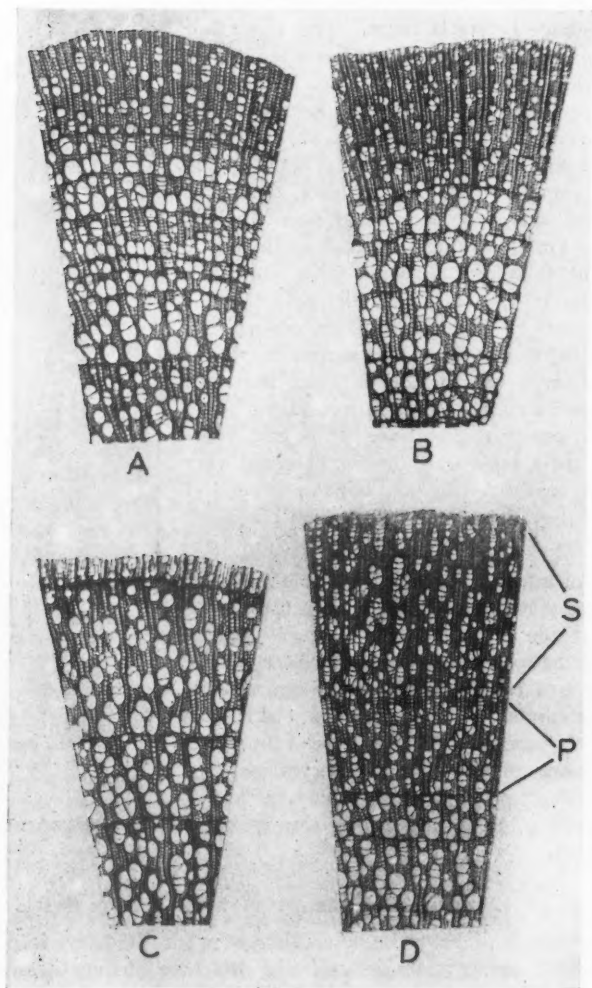


FIG. 4. A. Transverse section of root of aspen poplar, seven inches proximal to the shoot in Experiment A 1 (13"). Treated 16/5/34, collected 13/8/34. The outermost ring is the post-operative growth ring. $\times 24$. B. Transverse section of root of aspen poplar, seven inches proximal to the shoot in Experiment B 23 (13"). Treated 15/5/34, collected 13/8/34. The outermost ring is the post-operative growth ring. $\times 24$. C. Transverse section of root of aspen poplar, slightly less than one inch proximal to the shoot in Experiment C 1 (14"). Treated 16/5/34, collected 13/8/34. The outermost ring, which is very narrow, is the post-operative growth ring. $\times 24$. D. Transverse section of root of aspen poplar in Experiment B 2 (30"). Treated 15/5/34, collected 13/8/34. On 3/7/34 a ring with a longitudinal phloem bridge remaining was made in the root about nine inches proximal to the shoot, and the section illustrated was cut within the bridge. The xylem formed prior to and subsequent to wounding (3/7/34) is indicated by P and S respectively. $\times 24$.

NOTE.—The figure in brackets after the number of the experiment in the above, indicates the length in inches between the shoot-root crotch and the proximal complete ring.

treated as briefly as possible and they all lead to the same conclusion; *viz.*, that cambial activity in any but the basipetal direction was extremely limited in extent. In Stem Experiment A, the new wood formed in the untreated limb flowed round the base of the ringed limb in a loop, and sometimes there was no basifugal or acropetal development of cambial activity in the ringed limb. Usually, however, there was a slight development acropetally, and occasionally one did find an acropetal development for a few inches above the crotch, in the ringed limb. But at the most, the extent of development was very small. Stem Experiment A resembled rather closely the state of affairs obtaining in that method of pruning where a snag is left above the bud. Wray (12) has shown that, in such a case, cambial activity emanating from the bud flows downwards and obliquely around the stem, and there is no development in the acropetal direction in the snag. The snag, of course, dries out rapidly. Knight (5), on the other hand, observed a slight upward development of cambial activity in disbudded apple shoots, from the first growing branch below, and Sledge (7) reports that Swarbrick observed a very slow upward spread of new wood formation in a ringed apple shoot, from the first bud below, up to the lower edge of the ring.

In Stem Experiment B, cambial activity from the limb bearing developing growing points again tended to flow round the base of the ringed limb in a loop, but further progress was of course prevented by the complete ring below the crotch. The ultimate result was usually a marked "piling up" of new wood just above the crotch ring. This was particularly obvious in a thick band of wood running transversely round the base of the ringed limb. Cambial activity in the acropetal direction in the ringed limb was much the same as in Stem Experiment A. Sometimes there was none at all, usually there was a little, and occasionally cambial activity spread upwards for a few inches. But here again, cambial activity in the acropetal direction was at the most exceedingly feeble. In Stem Experiment C, a feeble gradient of cambial activity, spreading acropetally upwards in both limbs from the upper edge of the complete ring below the crotch, was the invariable result. Just above the crotch ring a very appreciable amount of xylem usually formed, but it was "piled up", and the gradient fell off very rapidly. Actually, Stem Experiment C yielded results very similar to Root Experiment C. There was, however, no comparison at all between the extent of development of cambial activity in Experiments A and B in stems, relative to that obtained in roots. In the stem experiments, all the tissues above a complete ring invariably died before the end of the growing season.

Discussion

In view of the mode of development of cambial activity emanating from sucker buds (arising after, or at all events having no vascular connection with the parent root prior to the operative procedure, and in regions of the root where the normal acropetal flow of cambial activity is not present) it is to be concluded that the marked development of cambial activity distal to a sucker

shoot, relative to that on the proximal side, is not determined by a previous re-orientation of the tissues at the base of the sucker bud. The answer, it would appear, is to be looked for in polarity of cambial development, and in this connection a number of points arise for discussion.

Jost (3, 4) was the first investigator to observe that cambial activity in the stem travels only in the basipetal direction. It has also been pointed out at various times by Priestley (6), by Wray (12) by Snow (8, 9, 10) and a few others. Snow (10) also reports that cambial activity develops only in the morphologically downward direction in roots of *Vicia Faba*. In fact this polar mode of development of cambial activity is now accepted as a general rule, with but few exceptions. However it is with the exceptions that the writer is mainly concerned. The observations of Knight and Swarbrick, of a feeble basifugal development of cambial activity in apple stems under certain conditions, have already been mentioned. These observations are confirmed by the writer's results with poplar stems. Here of course, the upward development of cambial activity is admittedly very feeble. However, in Root Experiment A, the development of cambial activity in the proximal direction is by no means feeble, and on the basis of this experiment alone, it would seem that polarity of cambial activity in poplar roots is very definitely not rigid or unconditional, and that any definition of polarity must be couched in terms of a *tendency* to develop in the distal rather than in the proximal direction. Fundamentally this may also apply to cambial activity in stems. The marked difference in the extent of development basifugally in stems, relative to that proximally in similar experiments with roots, might be conditioned by other factors, for example, water supply. A reasonable explanation of the results obtained in Root Experiment B is that the cambial stimulus that would normally travel acropetally is diverted proximally, which would also support a definition of polarity in terms of a tendency. The mode of development of new wood emanating from developing buds under the conditions previously described (Fig. 3) is of great interest. Actually, cambial activity at first seems to be inherently capable of developing in all directions possible, distally, laterally and proximally, and it looks almost as if the ultimate development distally were being conditioned by some factor not inherent in cambial activity as such.

Reference might also be made to the local basifugal development of cambial activity from the upper edge of a complete ring in stems, and the corresponding development proximal to a complete ring in roots. These are widely recognized exceptions to the general rule in regard to cambial development. But of still greater interest is the local development of cambial activity in the vicinity of a wound, where instead of a complete ring being made, a longitudinal phloem bridge is left. In the stem, there occurs a basifugal development of xylem formation from the upper edge of the wound, similar to that obtained when the ring is complete. Within the bridge, however, development is basipetal, and just below the bridge it is basipetal and lateral. A correspond-

ing type of development obtains in similarly treated roots. These remarks apply to cambial activity in the vicinity of wounds, independent of any normal cambial activity emanating from developing shoots. A more detailed account of cambial activity in relation to wounding will be published later.

Some recent observations by Elliott (2) are also worthy of mention. He has shown that in *Acer* cambial activity proceeds acropetally into the leaf from the junction of the lamina and petiole, and in *Castanea* acropetally along the petiole from its base into the lamina. At the same time there is the usual basipetal development of cambial activity down the shoot from the top of the petiole in *Acer* and from the bottom of the petiole in *Castanea*.

Now there is a possible danger of the idea of *rigid* polarity of cambial activity becoming almost a general law in the minds of some investigators, particularly so in view of the fact that Snow and LeFanu (11) have shown that an ether extract of urine promotes cambial activity, and the possibility that the hormone promoting cambial activity may be identical with the auxin causing cell elongation in the oat coleoptile, in which according to a number of investigators translocation of the auxin is strictly polar. The writer suggests in this connection that the fact that cambial activity does not or apparently cannot proceed in any but the morphologically downward direction, in some cases, does not necessarily mean that it cannot possibly develop in the opposite direction under any condition.

The fact that there was no reversal of the tissue orientations in relation to the wound with the longitudinal phloem bridge, made subsequent to the first operative procedure in Root Experiments A and B, is very puzzling. However, a possible explanation has been indicated and at all events the writer does not feel that his conclusion, that cambial activity is not rigidly and unconditionally polar, is rendered untenable because of the phenomenon just mentioned.

Recognition of the fact that polarity of cambial activity, which is but one of many polar phenomena in plants, constitutes a difficult problem is of course not new, and no pretence is made that the foregoing experiments indicate a solution of polarity of cambial activity in particular. However, definite experimental results have been obtained, on the basis of which the following conclusion is submitted for consideration; *viz.*, that cambial activity is polar in its development, when polarity is defined in terms of a *tendency* to develop in the morphologically downward direction, rather than in the morphologically upward direction. On the other hand, it may be suggested that cambial activity as a process is not inherently polar in its development, but is determined by some other factor. If however, this determining factor should be polarity of the organism as a whole, or polarity of some particular organ as a whole, then the two interpretations really become identical, and polarity of the organ or organism as a whole would have to be defined in terms similar to those suggested for cambial activity.

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STRIPE RUST, *PUCCINIA GLUMARUM*, IN CANADA¹

BY MARGARET NEWTON² AND T. JOHNSON³

Abstract

A study was made of the distribution of *Puccinia glumarum* (Schm.) Erikss. and Henn. in Canada, its specialization, host range, and reaction to environmental conditions. Unlike *Puccinia graminis* Pers., this rust has a limited distribution, being confined to British Columbia, Alberta, and the western half of Saskatchewan. The natural hosts include a number of native grasses, particularly *Hordeum jubatum* L. and certain species of *Agropyron*, *Elymus*, and *Bromus*. Wheat and barley also become infected although to a rather limited extent. Stripe rust collected on the above-mentioned hosts has been studied in the greenhouse and has in all cases shown ability to attack wheat varieties. In all instances where identification of physiologic forms was carried out the rust strains were classified as either form 8 or form 13 of wheat stripe rust, the latter form being the more common. The fact that the present authors have collected known physiologic forms of wheat stripe rust on species of *Hordeum*, *Elymus* and *Agropyron*, and have shown that forms 4, 6, 8 and 13 can attack seedling plants of *Hordeum*, *Agropyron*, and *Elymus* species throw a doubt on the existence of the *Hordei*, *Elymi*, and *Agropyri* varieties created by Eriksson.

Greenhouse studies showed that *P. glumarum* is extremely sensitive to environmental conditions, particularly temperature. The optimum for uredospore germination is 10° to 12° C., and for rust development 13° to 16° C. Varieties susceptible at from 10° to 16° C. developed resistance at higher temperatures, becoming extremely resistant at 25° C. On account of the sensitiveness of this rust to high temperatures it seems improbable that it will ever become thoroughly established in Manitoba and Saskatchewan, as in these two provinces the summer temperature is probably too high to permit its development.

Introduction

Stripe rust, *Puccinia glumarum* (Schm.) Erikss. and Henn., has a more limited distribution in Canada than the other cereal rusts, being confined to British Columbia, Alberta, and the western half of Saskatchewan. Collections have been made as far east as Whitewood, Saskatchewan, which is 102° W. longitude, or a little beyond the eastern limit reported for this rust in the United States by Humphrey *et al* (13). Some concern has been felt in Canada lest this rust might be slowly advancing eastward and that it would be merely a matter of time until it would become established throughout the prairie provinces of Canada. It seemed advisable, therefore, to ascertain what environmental factors influenced the spread of the organism, and whether or not more than one physiologic form of the organism was present. This study was begun in July, 1927.

Discovery and Host Range

In Canada *Puccinia glumarum* was first discovered by Fraser (5) in 1918, at Edmonton, Alberta, on *Hordeum jubatum* L. In 1924 it was reported on barley by Fraser and Connors (5) and in 1926 it was found on a number of wheat varieties by Sanford (24).

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Collections of the rust have been made, chiefly in British Columbia, by the present authors on the following species of grasses: *Agropyron repens* (L.) Beauv., *A. trachycaulum* (Link) Malte var. *unilaterale* (Vasey) Malte, [*A. Richardsonii* (Trin.) Schrad.], *A. Smithii* Rydb., *A. trachycaulum* (Link) Malte var. *typicum* Fernald [*A. tenerum* Vasey], *Bromus carinatus* Hook. & Arn. var. *Hookerianus* (Thurb.) Sheer, *B. ciliatus* L., *B. marginatus* Nees, *B. sitchensis* Bong., *Elymus glaucus* Buckley, *E. virescens* Piper, *Hordeum jubatum* L. var. *caespitosum* (Scribn.) Hitchc., and *H. jubatum* L. Several of the above-mentioned species have also been reported as hosts of stripe rust in Alberta by Sanford and Broadfoot (25, 27) who also include as hosts *A. trachycaulum* (Link) Malte [*A. caninum* (L.) Beauv.], *A. cristatum* (L.) Gaertn., *A. Dagnae* Grossh.*, *A. dasystachyum* (Hook.) Scribn., *A. desertorum* Schult.*, *A. rigidum* Beauv. [*A. elongatum* Host.] *A. Griffithsii* Scribn. & Smith, *A. pungens* Roem. & Schult*, *A. sibericum* (W.) Eichw.*, *A. spicatum* (Pursh.) Scribn. & Smith.

Studies on the Effect of Environmental Factors Upon the Spread of *Puccinia glumarum* in Western Canada

At the beginning of this study difficulties were encountered in establishing cultures of *Puccinia glumarum* in the greenhouse. Plants inoculated during the hot summer months flecked heavily but developed no pustules. Those inoculated in the autumn, when the temperature in the greenhouse was considerably lower than in the summer months, became heavily infected. It seemed fairly evident that the high temperature prevailing during the summer months was in some way responsible for the failure of the plants to become infected. An attempt was made, therefore, to determine the optimum temperature, for the germination of uredospores and for the best development of the organism within the tissues of the host plant.

INFLUENCE OF TEMPERATURE UPON THE GERMINATION OF UREDOSPORES

Uredospores freshly formed in the greenhouse on seedling leaves were germinated in hanging drops of tap water in Van Tieghem cells and in Syracuse watch glasses at six different temperatures ranging from a lower limit of from 2° to 3° C. to an upper limit of from 22° to 25° C. (Table I). At each temperature, from 2000 to 4000 spores were counted. Comparative tests were also made with uredospores of *Puccinia graminis Triticis* Erikss. and Henn. at the same temperatures.

In all the tests the best germination of the stripe-rust spores was consistently obtained at 10° to 12° C., while below 5° C. and above 20° C. there was a sharp decline in germination. It will be noticed that the germination percentages given in Table I are considerably lower than those of stem rust at all except the lowest temperature (2° to 3° C.). The germination percentages are, however, somewhat higher than those obtained by Raeder and Bever for *P. glumarum* (22), but lower than those reported by Wilhelm (34). The

* Species not native and probably not widespread in Western Canada.

TABLE I
A COMPARISON OF THE GERMINATION OF NEWLY FORMED UREDOSPORES OF
Puccinia glumarum AND *Puccinia graminis* *Tritici*

Temperature, °C.	<i>P. glumarum</i>		<i>P. graminis</i> <i>Tritici</i>	
	Number of tests	Germination, %	Number of tests	Germination, %
2 - 3	24	12	13	tr.
5 - 7	10	46	5	83
10 - 12	15	59	8	77
14 - 16	14	39	10	77
20 - 22	27	tr.	6	89
22 - 25	28	tr.	6	69

former, however, made no attempt to germinate spores of the same age, while the latter used spores that were all of approximately the same age. As the spores of *P. glumarum* are apparently very sensitive to environmental conditions, it seems very probable that no two workers could possibly obtain the same results unless the spores were produced and germinated under identical conditions.

Not only were the uredospores of *P. glumarum* less viable than were those of *P. graminis* but their range of temperature for germination appeared to be somewhat narrower. Good germination was secured only between 5° and 18° C. whereas the spores of *P. graminis* *Tritici* germinated freely between 5° and 25° C.

INFLUENCE OF TEMPERATURE AND HUMIDITY UPON THE LONGEVITY OF UREDOSPORES

During the hot summer months field cultures, approximately ten days old, from British Columbia and Alberta germinated very poorly, showing that the uredospores underwent a great loss of viability during transit. The sensitivity of uredospores of *P. glumarum* to environmental conditions has been commented upon by several investigators, Mehta (18) reported a germination of only 5% after storage for one month in the laboratory, and Wilhelm (34) stated that spores only eight days old showed a delay in germination and a loss of viability. Gassner and Straib (7) found that exposure of the spores of *P. glumarum* to direct sunlight at from 30° to 35° C. for four hours practically destroyed their viability but did not affect spores of *P. triticea* Erikss., *P. dispersa* Erikss., or *P. coronifera* Kleb.

The sensitiveness of the spores to external conditions and the difficulty of culturing the rust in the greenhouse during the three hot summer months made it imperative to devise a satisfactory method for preserving the cultures during the period unfavorable for cultural work. The experiments of Becker (2) had indicated 0° C. and 40% relative humidity as the optimum conditions of storage. Under these conditions she still found a portion of the spores germinable, at the end of 433 days. Raeder and Bever (22), however, found

the most satisfactory conditions for the storage of spores to be a temperature of from 9° to 13° C. and a relative humidity of 49%, under which conditions spores remained viable for a period of 88 days.

In the present study a number of tests were made to determine the longevity of uredospores of three physiologic forms of *P. glumarum* at a temperature of 5° C. and a relative humidity of 50%. The results of these tests are given in

TABLE II
PERCENTAGE GERMINATION OF UREDOSPORES OF THREE
PHYSIOLOGIC FORMS OF *Puccinia glumarum*
STORED AT 5° C. AND 50% RELATIVE
HUMIDITY FOR DIFFERENT PERIODS
(Germination based on a count of 1000 spores)

Physiologic form	No. of days uredospores in storage	Germination, %
13	60	14.6
	65	10.0
	70	4.0
	80	5.6
	90	3.6
	100	0
	110	trace
	150	0
	400	0
8	75	7.6
	80	2.0
	90	trace
	95	trace
	130	0
	400	0
4	65	4.9
	70	6.2
	75	3.4
	80	trace
	90	trace
	128	trace
	150	0
	400	0

Table II which shows that at the end of 75 days from 3 to 7% of the spores germinated while a trace of germination was secured after 128 days. That this relatively weak germination sufficed to cause infection was shown by the successful infection of ten wheat seedlings with spores of each of four physiologic forms that had been in storage for 95 days. In a repetition of this experiment a year later, all cultures in storage germinated sufficiently well to cause infection at the end of three months. It would seem, therefore, that freshly formed uredial material of *P. glumarum* can be stored with safety for at least three months, a period corresponding to the critical mid-summer period during which this rust can only be kept in culture in the greenhouse with extreme difficulty.

INFLUENCE OF TEMPERATURE UPON UREDIAL DEVELOPMENT

It has long been known that the reactions of many rusts are influenced by changes in environment, particularly by changes in temperature and light intensity. Waterhouse (33), in studying a number of the cereal rusts, found that "major differences in the rust reactions may be brought about by altering the environmental conditions under which the tests are made. Complete susceptibility under summer conditions may change to complete resistance under winter conditions". Similar fluctuations due to temperature changes were noted by Johnson (15) in the types of infection upon wheat infected with

P. graminis Tritici, and by Gordon (11) and Peturson (21) upon oats when infected with *P. graminis Avenae* Erikss. and Henn. and *P. coronata* Cda. respectively.

Experiments were therefore conducted to ascertain to what extent temperature influences the rust reactions of wheat varieties to *P. glumarum*.

While the work was still in progress Gassner and Straib (6) published results which showed that wheat varieties susceptible to *P. glumarum* at low temperatures become resistant or immune at moderately high temperatures, results which agreed with our own observations (19).

Experimental Methods

The plants used for these experiments were grown in duplicate sets and kept at ordinary greenhouse temperature prior to inoculation. Inoculations were made when the plants were in the first-leaf stage. The methods of inoculating and culturing the rust, as well as the symbols used in recording the rust reactions, were, with certain modifications, similar to those described by Hungerford and Owens (14), which were, in turn, adaptations of those first used by Stakman and Piemeisel (29) for stem rust. The Arabic numerals "0" to "4" indicate the type of infection in order of increasing severity. A description of these infection types is as follows:

Resistant Class

- Type 0(n) No uredia; dead necrotic areas often present.
- Type 1 Uredia few or minute, generally surrounded by dead areas; portions of leaves sometimes killed or discolored.
- Type 2 Uredia normal in appearance, but few and scattered; discoloration of leaf tissues common.

Susceptible Class

- Type 3 Uredia normal, moderately abundant; little discoloration of leaf tissue.
- Type 4 Uredia normal and very abundant, appearing uniformly over surface of inoculated leaf; no discoloration in early stages of infection.

The signs (=), (-), and (\pm), are used to indicate quantitative variations in the above types.

Influence of Two Different Temperatures Upon Infection Types

Nine wheat varieties, Acme, Arnautka, Little Club, Mindum, Spelmar, and Vernal were inoculated with *P. glumarum* forms 4, 8, and 13. One set of plants was kept at 25.3° C. and the other at 12.9° C. Above or below either of these temperatures, the variation was not more than 2°.

The results presented in Table III show that at 25.3° C. all the hosts tested to the three physiologic forms were completely resistant, while at 12.9° C.

TABLE III

THE RELATIVE REACTIONS OF WHEAT VARIETIES INOCULATED WITH *Puccinia glumarum*, FORMS 4, 8, AND 13, AND KEPT AT TWO DIFFERENT TEMPERATURES

Variety	Form	Number of plants inoculated	Number of plants infected	Reactions at	
				25.3° C.	12.9° C.
Little Club	4	20	20	Resistant	Susceptible
Spelmar	4	22	21	Resistant	Susceptible
Vernal	4	26	26	Resistant	Susceptible
Acme	8	21	18	Resistant	Susceptible
Arnautka	8	25	24	Resistant	Susceptible
Brevit	8	24	22	Resistant	Susceptible
Chul	8	22	22	Resistant	Susceptible
Mindum	8	26	23	Resistant	Susceptible
Prelude	8	26	25	Resistant	Susceptible
Vernal	8	20	20	Resistant	Susceptible
Acme	13	22	22	Resistant	Susceptible
Chul	13	24	23	Resistant	Susceptible
Mindum	13	23	22	Resistant	Susceptible
Prelude	13	24	24	Resistant	Susceptible

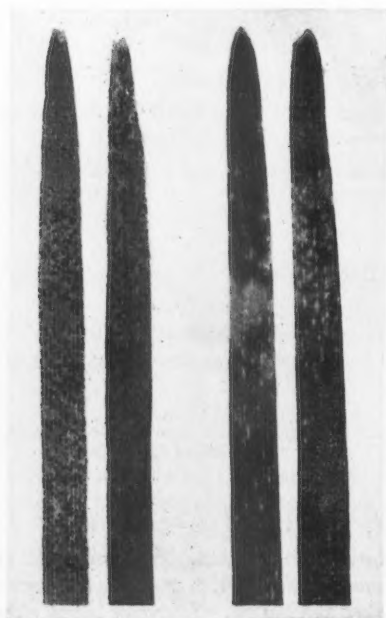


FIG. 1. Reaction of Chul wheat to *P. glumarum*, form 13, at 12.9° C. (left) and at 25.3° C. (right).

they were completely susceptible. At the high temperature (25.3° C.) the plants flecked heavily but produced practically no uredia, but at the low temperature (12.9° C.) abundant uredia were produced. The reaction of Chul wheat to form 13 at 25.3° C. and 12.9° C. is shown by means of a photograph (Fig. 1).

In order to ascertain if the mycelium in the heavily-flecked plants was still alive and capable of further development under cooler conditions, the heavily flecked plants were placed for ten days in a section of the greenhouse maintained at 12.9° C. Plants with only flecks developed no uredia, a result which showed that the mycelium had died at the high temperature (25.3° C.). Those with flecks plus minute uredia now developed normal-sized uredia. In these plants the mycelium was

apparently injured at a temperature of 25.3° C. but not completely destroyed. However, as only a small number of plants kept in the hot greenhouse (25.3° C.) ever bore uredia, it seems safe to assume that the mycelium of stripe rust is usually killed in plants kept continuously ten days or more at that temperature.

Effect of Temperature on Infection Type

(a) *When plants are kept for a definite number of days at one temperature and then transferred to another*

Some experiments were carried out to determine the effect of exposing wheat plants, which are susceptible to stripe rust, to a relatively high temperature before transferring them to a relatively low temperature or *vice versa*. In the month of March, 24 pots of Prelude wheat were inoculated with form 4. After removal from the incubation chambers, 13 of the pots were placed in a section of the greenhouse maintained at a temperature of 22.7° C. and 13 in a section at a temperature of 13.7° C. At the end of one day, and on each succeeding day for 11 days, one pot was transferred from the higher to the lower temperature, and one from the lower to the higher temperature. One pot was kept as a control in each section. The results indicate that the longer the infected wheat plants were kept at a temperature of 22.7° C. before they were transferred to a temperature of 13.7° C., the greater was their resistance (Table IV) and, conversely, the longer they were kept at a temperature of 13.7° C. before they were transferred to a temperature of 22.7° C., the greater was their susceptibility.

TABLE IV

THE TYPES OF INFECTION PRODUCED BY *Puccinia glumarum*, FORM 4, ON PRELUDE WHEAT WHEN PLANTS WERE KEPT FOR DIFFERENT NUMBERS OF DAYS AT A TEMPERATURE OF 22.7° C. AND THEN TRANSFERRED TO A TEMPERATURE OF 13.7° C.

Days at		Infection results	Reaction
22.7° C.	13.7° C.		
1	11	$\frac{11}{12}(4)$	Susceptible
2	10	$\frac{1}{3}(4)$ $\frac{1}{3}(n)$	Susceptible
3	9	$\frac{8}{12}(3)$	Susceptible
4	8	$\frac{5}{12}(3)$ $\frac{5}{12}(2)$ $\frac{2}{12}(n)$	Semi-resistant
5	7	$\frac{4}{12}(3)$ $\frac{4}{12}(2)$ $\frac{4}{12}(n)$	Semi-resistant
6	6	$\frac{3}{12}(2)$ $\frac{3}{12}(1)$	Resistant
7	5	$\frac{2}{12}(1)$ $\frac{2}{12}(n)$	Resistant
8	4	$\frac{1}{12}(n)$	Resistant
9	3	$\frac{1}{12}(n)$	Resistant
10	2	$\frac{1}{12}(n)$	Resistant
11	1	$\frac{1}{12}(n)$	Resistant
Kept continuously at 22.7° C.		$\frac{1}{12}(n)$	Resistant
Kept continuously at 13.7° C.		$\frac{1}{12}(4)$	Susceptible

Explanatory note.—The infection types are enclosed in brackets. The figures preceding the infection types indicate the number of leaves infected, e.g., $\frac{5}{12}(3)$ $\frac{5}{12}(2)$ $\frac{2}{12}(n)$ shows that 5 out of 12 leaves bore a (3) type of infection, 4 out of 12 leaves, a (2) type of infection, and 2 out of 12, necrotic flecks.

(b) *When plants are kept for a definite number of hours each day at one temperature and then transferred to another*

Since, however, the real object of these temperature studies was to find out whether stripe rust was likely to become prevalent in the great wheat-growing areas of Manitoba, Saskatchewan, and Alberta, some experiments were carried out to ascertain how many hours of high temperature the wheat plants could tolerate daily and still permit a normal type of infection to develop; for it seemed possible that, although during the growing season the night temperatures in Manitoba, Saskatchewan, and Alberta are always relatively low, the day temperatures are generally fairly high and might inhibit all stripe rust development.

Fourteen pots of Prelude wheat were inoculated with form 4 and placed in a greenhouse maintained at 12.9° C. They were carefully numbered and arranged in seven sets of two pots each. Set 1 was kept daily for 8 hours in this greenhouse and was then transferred for 16 hours to a greenhouse maintained at 25.3° C. This procedure was repeated for 17 days. Sets 2, 3, 4, and 5, were likewise transferred daily from one temperature to the other but for different lengths of time. The period during which any one of these sets was kept in either greenhouse is given in Table V. Sets 6 and 7 were used as controls. The former was kept continuously at 12.9° C. and the latter at 25.3° C. The experiment was repeated later using a different physiologic form, a different variety, and two other temperatures, with quite similar results.

TABLE V

THE TYPES OF INFECTION PRODUCED BY *Puccinia glumarum*, FORM 4, ON PRELUDE WHEAT WHEN PLANTS WERE KEPT FOR A DEFINITE NUMBER OF HOURS EACH DAY AT 12.9° C. AND THEN TRANSFERRED TO A TEMPERATURE OF 25.3° C. FOR THE REMAINDER OF THE DAY

Plants	Hours at		Infection Results	Reaction
	12.9° C.	25.3° C.		
Set 1	8	16	$\frac{3}{12}(n)$	Resistant
Set 2	10	14	$\frac{2}{12}(n)$	Resistant
Set 3	12	12	$\frac{1}{12}(3)$ $\frac{1}{12}(2) -$	Resistant
Set 4	14	10	$\frac{1}{12}(2)$ $\frac{2}{12}(3) -$	Semi-resistant
Set 5	16	8	$\frac{1}{12}(4) -$	Susceptible
Set 6	Kept continuously at 12.9° C.		$\frac{3}{12}(4)$	Susceptible
Set 7	Kept continuously at 25.3° C.		$\frac{1}{12}(n)$	Resistant

From Table V it will be seen that plants kept at (25.3° C.) for 12 hours or more daily became resistant while those for 8 hours or less were susceptible; the ones held at the higher temperature for 10 hours were intermediate in reaction, or semi-resistant.

A study was made of the temperature prevailing in the prairie provinces and British Columbia to ascertain if some parallel could be found between the behavior of the rust in the greenhouse at known temperatures and its development under field conditions. In Table VI are given the mean daily

TABLE VI
MEAN DAILY MAXIMUM AND MINIMUM TEMPERATURE, TOGETHER WITH AN AVERAGE OF THE EXTREME HIGHEST AND EXTREME LOWEST RECORDED
FOR EACH MONTH, IN CERTAIN DISTRICTS IN BRITISH COLUMBIA, ALBERTA, SASKATCHEWAN, AND MANITOBA, DURING
JULY AND AUGUST, FOR THE FIFTEEN YEAR PERIOD, 1919 TO 1933

District	Temperature, °F.							
	July				August			
	Mean daily max.	Mean daily min.	Mean extreme highest	Mean extreme lowest	Mean daily max.	Mean daily min.	Mean extreme highest	Mean extreme lowest
<i>British Columbia</i>								
Southeast Vancouver Island	72.3	51.7	93.0	39.7	72.7	51.7	93.9	41.0
Lower Fraser River	75.3	53.3	93.4	41.7	74.9	53.5	93.1	42.0
<i>Alberta</i>								
North Saskatchewan River	75.5	47.3	98.7	26.8	72.6	45.0	94.9	22.2
The Bow River	78.7	49.8	101.0	29.2	76.9	47.1	98.3	25.9
<i>Saskatchewan</i>								
Qu'Appelle River	79.3	51.7	103.5	32.9	77.4	48.4	100.1	28.4
South Saskatchewan River	81.0	51.3	100.1	32.0	78.7	48.5	98.3	28.7
North Saskatchewan River	77.8	49.6	98.5	31.9	75.4	46.6	94.9	27.5
The Saskatchewan Forks	78.8	52.3	98.1	35.1	76.3	48.5	96.1	30.4
<i>Manitoba</i>								
Qu'Appelle and Assiniboine Rivers	79.3	53.6	100.4	35.1	77.7	50.3	98.0	29.9
The Red River	79.8	55.4	97.5	34.9	78.2	52.1	97.7	30.1

The temperatures in this table are expressed in Fahrenheit, the scale used in Canadian meteorological records.

minimum and maximum temperatures for July and August, together with the average of the extreme highest and extreme lowest temperatures, in certain districts in British Columbia, Alberta, Saskatchewan, and Manitoba for the 15-year period 1919 to 1933.

It will be seen from Table VI that, in July as well as in August, the mean minimum daily temperature is somewhat lower in Alberta than in Saskatchewan, and lower in Saskatchewan than in Manitoba. For the same districts of the prairie provinces, with the exception of South Saskatchewan River, the mean daily maximum temperatures are in the same order, although the differences are only slight. In British Columbia, where the rust persists through the summer, both the mean daily maximum and the mean extreme highest temperatures for the summer months are considerably lower than in the prairie provinces.

The temperature conditions prevailing in the prairie provinces during the summer months and the greenhouse temperatures recorded in Table V are probably not strictly comparable in their effects on host and parasite, as the plants in the greenhouse were grown at two definite levels of temperature whereas in the field the daily temperatures vary from minimum to maximum. Nevertheless it is suggestive that when plants are kept in the greenhouse for 12 hours at a low temperature (slightly higher than the mean daily minimum for July in most districts of the prairie provinces), and for the remaining 12 hours of the day at a high temperature (slightly lower than the mean daily maximum for these provinces), these plants become definitely resistant to stripe rust. The fact that the mean extreme highest summer temperatures (Table VI) rise far above any of the greenhouse temperatures used—the highest was 25.3° C. (77.5° F.)—is an additional reason for supposing that the summer temperatures in the prairie provinces are inhibitory to the growth of the rust during that period. This conclusion is in accord with that arrived at by Sanford and Broadfoot (26) who assume that the stripe rust infestation occurring in Alberta in the autumn months has its origin in wind-borne spores that drift in from the adjoining states of Montana, Idaho, and Washington, rather than in local infections which have survived from the previous year through the severe winter and the hot summer months. Field observations seem to support both of these conclusions, for stripe rust has never been found in Manitoba or the eastern half of Saskatchewan, although it occurs rarely in western Saskatchewan and is present every year in Alberta.

It is conceivable that in an unusually cool summer stripe rust might become more prevalent than it has hitherto been known to be. There is also the possibility that there may exist, or come into existence, a form which is less sensitive to high temperatures than the forms that have been studied in these experiments.

Physiologic Specialization in *Puccinia glumarum*

Physiologic forms of *Puccinia glumarum* were isolated for the first time in Canada in 1932 (20). Their presence in America, however, had been suggested at an earlier date by the work of Hungerford and Owens (14). These

authors found that when *Bromus sterilis* was inoculated with uredospores from *Hordeum jubatum* the former remained resistant, but when it was inoculated with spores from *Bromus marginatus* or *Elymus glaucus* it proved highly susceptible, and they decided that either two forms of *P. glumarum* were involved or that two strains of *Bromus sterilis* had been used. In 1934 Bever (3) was able to show definitely that two forms of *P. glumarum* of wheat, forms 19 and 28*, were present in the United States.

From 1925 to 1928 Rudorf (23) tested a number of wheat varieties to *P. glumarum* in Germany, and found that some of the wheat varieties which Hungerford had classified as resistant to this rust in America were susceptible in Germany. He therefore concluded that the form of *P. glumarum* occurring in Germany was distinct from that found in the United States. In 1930, Allison and Isenbeck (1) demonstrated the presence of four physiologic forms of *P. glumarum* in Europe. About the same time there appeared an article by Gassner and Straib (8) in which they were able to prove the existence of two physiologic forms in west middle Europe, and a few months later Wilhelm (34) reported the existence of five physiologic forms of the organism, three of which he isolated from collections made in Germany, one from France, and one from Sweden.

In Canada systematic annual surveys for physiologic forms of *P. glumarum* were not carried out, but since 1927 collections from wheat, *Aegilops*, barley, and a number of grasses have been studied (Table VII). These collections were made in British Columbia, Alberta, and Saskatchewan. For comparative purposes, two collections of rust from the United States and two from England were studied, together with two from Germany. The separation of the rust cultures into definite physiologic forms was accomplished by means of the wheat varieties selected by Gassner and Straib (9) as differential hosts for *P. glumarum*.

In order to be sure that the reactions of the different hosts were based on race difference and were not the results of environmental influences all tests were made in a greenhouse kept at a temperature of 16° C.

DISTRIBUTION AND INFECTION CAPABILITIES OF THE FORMS ISOLATED

The physiologic forms isolated can be seen from Table VII, which gives the hosts upon which the several forms were collected, the year and the place of collection, and a summary of the infection types of each form on all the differential hosts. From this table it is clear that four physiologic forms of *P. glumarum*, forms 4, 6, 8, and 13, were present in the material studied. Of these forms 8 and 13 were isolated from the collections of rust made in Canada; form 6, from Germany; and form 4, from England. Of the two collections from the United States, the one from Berkeley, California, proved to be form 13 and the one from Moscow, Idaho, form 8.

*These numbers do not appear in the paper cited but were supplied recently to the author by Dr. Bever.

Of the two forms isolated in Canada the less virulent one, form 13, is much more prevalent than form 8, being represented by seventeen of the eighteen Canadian collections studied between 1927 and 1935. Although form 13 has a wider distribution in Canada than form 8, it has not yet been found in Europe.

RESISTANCE OF CEREALS AND GRASSES

Resistance of Wheat Varieties

With a view to discovering wheat that might be of value in breeding for resistance to stripe rust, if that became necessary, 52 varieties of wheat were tested to the four physiologic forms. The results of this test are given in Table VIII. In this table the varieties are arranged in groups, each group having something more or less in common with respect to the type of infection produced upon the varieties by the four physiologic forms. In the first group,

TABLE VIII

THE MEAN INFECTION TYPES OF FOUR PHYSIOLOGIC FORMS OF *Puccinia glumarum* ON 52 WHEAT VARIETIES AND HYBRID STRAINS IN THE SEEDLING STAGE

Varieties tested		Origin of physiologic form			
		Germany, Form 4	England, Form 6	Canada	
				Form 8	Form 13
Acme	R.L. 566	4-	4-	4-	4-
Chabot		4-	4-	4-	4-
Chul	R.L. 543	4-	4-	4-	4-
H-44-24	R.L. 229	3+	3+	3+	3
Hope	R.L. 209	3+	3+	3+	3
Hussar	C.I. 4843-1-5	3+	3+	3	3
Kanred × Marquis	R.L. 226	3+	3+	3+	3+
Kota	R.L. 571	3-	3-	3-	3-
Kubanka	R.L. 565	3+	3+	3	3
Malakoff	C.I. 4898-4	3+	3+	3+	3+
Mindum	R.L. 568	3+	3+	3+	3+
Monad	R.L. 205	3+	3+	3+	3
Norka	C.I. 4377-2-1	4-	4-	4-	4-
Parker's	R.L. 71	4-	3+	3+	3-
Pentad	R.L. 203	3+	3+	3-	3-
Prelude	R.L. 25	4-	4-	4-	4-
Reliance	R.L. 198	4-	4-	4-	3+
Reward	R.L. 79	4-	3+	4-	4-
Ruby	R.L. 12	4-	3+	4-	4-
Supreme	R.L. 77	4-	4-	3+	3+
Arnautka	R.L. 570	3+	3+	3+	1+
Axminster	R.L. 75	3+	3+	3	2-
Black Persian	R.L. 388	3	3+	3	2-
Brevit	C.I. 3778-1	3+	3	3+	2+
Democrat	C.I. 3384-3-2	3+	3+	3+	1
Hard Federation	R.L. 921	3+	3+	3+	0(n)
Little Club	R.L. 223	3+	3	3+	2-
Marquis	R.L. 572	4-	3+	3=	2-
Power	R.L. 202	3+	3+	3+	2+
Sevier × Dicklow	R.L. 368	4-	3+	3+	2
Spelmar	R.L. 569	3+	3+	3+	2+
Vernal	R.L. 567	4-	4-	4-	1-

TABLE VIII—*Concluded*

THE MEAN INFECTION TYPES OF FOUR PHYSIOLOGIC FORMS OF *Puccinia glumarum* ON 52 WHEAT VARIETIES AND HYBRID STRAINS IN THE SEEDLING STAGE

Varieties tested		Origin of physiologic form			
		Germany, Form 4	England, Form 6	Canada	
				Form 8	Form 13
Loros	C.I. 3779-4-1	3+	3=	2	2-
N.D. 1656	R.L. 126	3	3	2	2-
Pelissier	R.L. 145	3	3=	1+	1+
Red Fife	R.L. 22	4-	3+	2-	1
Renfrew	R.L. 135	3+	3+	2+	1+
Similis	C.I. 3747-1-1	3	3	1	2-
Svalofs Panzer III		3=	3+	2-	0(n)
Golden Drop		3+	0(n)	0(n)	0(n)
Vilmorins Blé du bon Fermier		4-	0(n)	0(n)	0(n)
Vilmorins Blé gros bleu		3+	1+	0(n)	0(n)
Carina	C.I. 3756-3-5	1-	1+	1	1
Ceres	R.L. 127	2-	2+	2-	2-
Einkorn	R.L. 227	2+	2	2+	2+
Garnet	R.L. 15	0(n)	0(n)	0(n)	0(n)
Iumillo	R.L. 7	1+	1-	1+	1-
Khapli	R.L. 563	2	2	2	0(n)
Marquillo	R.L. 132	1-	1+	1-	0(n)
Mediterranean	C.I. 3384-3-2	2	2+	2	2-
Quality	R.L. 133	1-	1+	0(n)	1-
Rieti		2+	—	2+	0(n)

¹ Accession numbers of Rust Research Laboratory.

for example, all the varieties listed are susceptible to the four forms used and bear a "3" or "4" type of infection; in the second group, the varieties are susceptible to three of the four forms; in the third group, they are susceptible to two of the forms; in the fourth group they are susceptible to only one of the four physiologic forms; while in the fifth group, the varieties are resistant to all four physiologic forms. Genetic material bearing the necessary factors for rust resistance is therefore readily accessible to the plant breeder, should such material be required at any time.

Resistance of Barley Varieties

In the early stages of this work it was shown (16) that stripe rust collected on *Hordeum jubatum* was able to cause heavy infections on wheat seedlings in the greenhouse. Later, in 1931, stripe rust collected on O.A.C. 21 barley at Olds, Alberta, caused heavy infections on two of the wheat differential varieties inoculated by it (20). The susceptible reaction of wheat to rust from these sources suggested the possibility that the stripe rust present in Western Canada was capable of parasitizing both wheat and *Hordeum* species. If such were the case there would be reason to doubt the existence of specialized *Tritici* and *Hordei* races of this rust. Accordingly it was decided to test the

reaction of a number of barley varieties to the four available physiologic forms of stripe rust of wheat. The reactions of nine barley varieties to forms 4, 6, 8, and 13 are given in Table IX, from which it is evident that three of the varieties, Glabron, O.A.C. 21, and Success are moderately susceptible to all the four forms.

TABLE IX
THE MEAN TYPES OF INFECTION PRODUCED BY FOUR
PHYSIOLOGIC FORMS OF *Puccinia glumarum* ON
SEEDLINGS OF NINE BARLEY VARIETIES

Variety tested	Physiologic form			
	4	6	8	13
Bay Brewing	1—	0(n)	0(n)	0(n)
Glabron	3—	3—	3—	3—
O.A.C. 21	3—	3—	3—	3—
Peatland	0(n)	0(n)	0(n)	0(n)
Plumage Archer	0(n)	0(n)	0(n)	0(n)
Success	3—	3—	3—	3—
Trebi	0(n)	0(n)	0(n)	0(n)
Velvet	1—	0(n)	1—	0(n)
Wisconsin 38	2—	2—	2—	2—

Resistance of Grasses

In view of the results obtained with barley varieties, it seemed desirable to study the pathogenicity of the same forms towards a number of the native grasses, particularly those of the genera *Agropyron* and *Elymus* which, according to Eriksson (4), harbor the *Agropyri* and *Elymi* races of stripe rust. The results of these tests, which were carried out in the greenhouse with seedling plants, are incorporated in Table X.

TABLE X
REACTIONS OF CERTAIN GRASSES IN THE SEEDLING STAGE TO FOUR PHYSIOLOGIC
FORMS OF *Puccinia glumarum*

Grass species tested	Physiologic form			
	4	6	8	13
<i>Agropyron cristatum</i> (Shreb.) Gaertn.	S & R	S & R	S & R	S
<i>A. dasystachyum</i> (Hook.) Vasey	S	S	S	S
<i>A. Griffithsii</i> Scribn. & Sm.	S	S	S	S
<i>A. repens</i> (L.) Beauv.	O(S)	O(S)	O	O
<i>A. repens</i> forma <i>setiferum</i> Fern.	O(S)	O(S)	O	O(S)
<i>A. trachycaulum</i> (Link) Malte var. <i>unilaterale</i> (Vasey) Malte.	S	S	S	S
<i>A. smithii</i> Rydb.	O(S)	O	O(S)	O
<i>A. trachycaulum</i> (Link) Malte var. <i>typicum</i> Fern.	S	S	S	S
<i>Bromus altissimus</i> Pursh.	R	R(S)	R	R
<i>B. ciliatus</i> L.	R(MS)	R	O	R & MS
<i>B. inermis</i> Leyss.	O	R	O	O
<i>B. marginatus</i> Nees.	O	O(S)	R	O(MS)
<i>B. purgans</i> L.	O	R	R	R
<i>B. stichensis</i> Bong.	R	R	R	R
<i>B. sterilis</i> L.	R	R	R	O
<i>Elymus canadensis</i> L.	S(R)	S & R	S	S
<i>E. curvatus</i> Piper	R(S)	R(S)	O(S)	R(S)
<i>E. dahuricus</i> Turcz.	S	S	S	S
<i>E. glaucus</i> Buckley	R	R	R	R(S)
<i>E. innovatus</i> Beal.	R	R	R	R
<i>E. virginicus</i> L.	S & R	S & R	S & R	R(S)
<i>Hordeum jubatum</i> L.	S	S	S	S
<i>H. murinum</i> L.	O(R)	O	O	O

Explanation of symbols: O = immune; R = resistant; MS = moderately susceptible; S = susceptible; S & R = some plants susceptible; some resistant; brackets () indicate that only very few plants showed reaction included.

Agropyron dasystachyum, *A. Griffithsii*, *A. trachycaulum* var. *unilaterale*, *A. trachycaulum* var. *typicum*, and *A. cristatum* proved rather highly susceptible to all of the four physiologic forms. The remaining *Agropyron* species were chiefly immune but possessed occasional susceptible plants.

Of the *Elymus* species tested, *Elymus dahuricus* and *E. canadensis* showed the greatest degree of susceptibility, the latter, however, exhibiting a small proportion of plants resistant to the two European forms. *Elymus curvatus* and *E. virginicus* were heterogeneous in reaction to each of the four forms, the reactions of individual seedlings varying from resistance to complete susceptibility. *E. glaucus* and *E. innovatus* proved highly resistant.

Of the other grasses tested the *Bromus* species were either immune or rather highly resistant with, however, a few susceptible plants in certain species. *Hordeum jubatum* was completely susceptible to all of the four forms while *Hordeum murinum* appeared to be immune.

THE QUESTION OF SPECIALIZED FORMS OR VARIETIES IN STRIPE RUST

The reactions of barley varieties and grasses to the four physiologic forms mentioned above have an obvious bearing on the question of the specialization of *Puccinia glumarum*. The fact that certain varieties of *Hordeum vulgare* and certain species of *Agropyron* and *Elymus* proved susceptible to the so-called *Tritici* race calls into question Eriksson's (4) division of this rust into the five specialized varieties *Tritici*, *Hordei*, *Secalis*, *Agropyri*, and *Elymi*. It is obvious that if the rust were thus specialized the *Tritici* variety should not be capable of attacking species of *Hordeum*, *Agropyron*, and *Elymus*, even as seedling plants.

Apart from the seedling reactions mentioned above there is available certain other evidence bearing on this question. Sanford and Broadfoot (27) state that *Hordeum jubatum* and *Agropyron dasystachyum* are the principal hosts of *P. glumarum* in Alberta. The present authors have during the past few years established cultures in the greenhouse from 11 collections on *H. jubatum*, 1 collection on *H. vulgare* (O.A.C. 21), 5 collections on *Agropyron trachycaulum* var. *unilaterale*, 1 collection on *Elymus* sp., 1 collection on *Agropyron repens*, and 1 collection on *Agropyron trachycaulum* var. *typicum*. Although the physiologic form present was not in all instances identified, it was demonstrated that every one of the cultures was capable of attacking wheat varieties. Cultures capable of attacking wheat seedlings were also secured from field collections made on *Aegilops cylindrica*, *Bromus ciliatus*, and *Bromus sitchensis*.

In certain cases the physiologic form present was identified (*Vide* Table VII). Thus collections on *Agropyron trachycaulum* var. *unilaterale* and *Aegilops cylindrica* were identified as form 8. Collections on *Agropyron trachycaulum* var. *unilaterale*, *Hordeum jubatum*, *Hordeum vulgare* (O.A.C. 21), *Elymus* sp., *Bromus ciliatus*, *Bromus marginatus*, and *Bromus sitchensis* were identified as form 13.

The fact that the present authors have collected known physiologic forms of wheat stripe rust on species of *Hordeum*, *Elymus*, and *Agropyron*, and have shown that forms 4, 6, 8, and 13 can attack seedling plants of *Hordeum*, *Agropyron*, and *Elymus* species throws a doubt on the existence of the *Hordei*, *Elymi*, and *Agropyri* varieties created by Eriksson.

A review of the literature shows, furthermore, that considerable evidence leading to a similar conclusion has been gathered by other workers. Treboux (32) showed, in 1912, that spores collected on *Agropyron repens* were capable of infecting *Triticum vulgare*, *Hordeum vulgare*, and *Bromus mollis*. Hungerford and Owens (14) in 1923, found that the specialized variety from wheat was able to infect a number of species of *Bromus*, *Agropyron*, *Hordeum*, and *Elymus* as well as rye and to a slight extent barley. Within the last three or four years further confirmation has been secured. Hassebrauk (12) showed that form 4 of *P. glumarum Tritici* infected species of *Secale* and *Agropyron* as well as a species of *Elymus* and concluded that the specialized forms of Eriksson were not so sharply fixed as was supposed formerly. Gassner and Straib (10) collected form 4 of *P. glumarum Tritici* on barley and on *Agropyron repens* and showed furthermore that certain varieties of barley and rye were susceptible, and *Agropyron repens* at least partially susceptible, to the majority of the known physiologic forms of *P. glumarum Tritici*. On the basis of this work they concluded that Eriksson's division of *P. glumarum* into five specialized varieties was not justifiable. According to a later paper by Straib (31) two of the more recently discovered physiologic forms—forms 23 and 24—attack barley varieties more vigorously than wheat. He does not, however, consider them as representatives of a distinct *Hordei* variety of the rust. He prefers to look upon stripe rust as a species consisting of a series of closely related specialized forms of which these two forms represent the one extreme while the other is represented by physiologic forms which attack wheat varieties more vigorously than barley (30).

Discussion

The limited distribution of *Puccinia glumarum* in Western Canada presents a problem of considerable interest to phytopathologists. Stripe rust is present annually in Alberta on certain grasses and to a slight extent on wheat. Its presence there and its gradual diminution in an easterly direction raise the question of the reason for its limited spread towards the east. The reason is obviously not lack of suitable host plants in the more easterly part of the prairie provinces as the most congenial grass host, *Hordeum jubatum*, is ubiquitous. It is probable, therefore, that the reason is rather to be sought in the climatic conditions prevailing through the growing season. Fraser* and Sanford and Broadfoot (26) have shown that the uredospores are capable, at least occasionally, of surviving the winter in Alberta but, as the last-mentioned authors point out, the further spread of the rust from such survivals is extremely doubtful. They conclude, therefore, that the source of the

* Unpublished data by Prof. W. P. Fraser, University of Saskatchewan, Saskatoon, Saskatchewan.

rust infestation which occurs annually in Alberta during the latter part of August and September is to be sought in wind-borne spores from the adjoining States of Montana, Idaho, and Washington.

The extreme sensitiveness of *P. glumarum* in the greenhouse to even moderately high temperatures makes it very probable that the high day temperatures which prevail in the prairie provinces during the summer months prevent the growth of the rust during that period. Greenhouse experiments showed that a temperature of 25° C. (77° F.) for from 10 to 12 hours each day rendered a susceptible host plant resistant to the rust, even when the temperature during the remainder of the day was congenial to both host and parasite. Even if the rust were able to germinate and infect a congenial host under the conditions of temperature that prevail in the summer, it is not improbable that the host plant would be rendered resistant by the high day temperatures which are common in these provinces. It is only in the autumn that stripe rust becomes prevalent in Alberta, the spread coinciding with the shortening of the day and the lowering of the day temperature. These changes in length of day and temperature are, however, so uniform in any given latitude of the prairie region that it is difficult to see how temperature differences could be invoked to explain the limited spread of the rust eastwards. It is probable, as is indeed pointed out by Sanford and Broadfoot (26), that the limited amount of inoculum produced in the stripe rust regions is not sufficient to disseminate the rust very far eastwards before the spread is terminated by the end of the short autumn season.

The behavior of the rust in British Columbia may likewise be interpreted on the basis of temperature conditions. Stripe rust is most abundant during the spring and autumn. The summer temperatures, although lower than those prevailing in the prairie provinces, nevertheless rise above the optimum for rust development, and the rust decreases in abundance during the mid-summer period. With the lower temperatures prevailing in the autumn months the amount of rust again increases. The fluctuation in the amount of stripe rust during these seasons is not likely due solely to temperature conditions. Differences in precipitation undoubtedly play a part. It is probable, however, that the rise in temperature during July and August is one of the chief factors limiting the distribution of stripe rust in that province.

The work reported in the present paper has also a bearing on the question of the specialization of *Puccinia glumarum* which Eriksson (4) subdivided into the five specialized varieties *Tritici*, *Hordei*, *Secalis*, *Agropyri* and *Elymi*. It has been demonstrated that known physiologic forms of wheat stripe rust occur in nature on species of *Hordeum*, *Agropyron*, *Bromus* and *Elymus* and further that forms 4, 6, 8, and 13 are able to attack seedling plants of species of *Hordeum*, *Agropyron*, and *Elymus*. In view of these facts and evidence of a similar nature gathered by other workers in Europe and America, it would seem advisable to disregard Eriksson's division of this rust into five specialized varieties as has, indeed, been suggested by Gassner and Straib (10) and to refer to this rust merely by the binomial *Puccinia glumarum* (Schmidt) Erikss. and Henn.

There can, however, be no question that *P. glumarum* is specialized into a number of physiologic forms which can be detected by the reactions of differential wheat varieties, as was first suggested by Rudolf (23) who found that wheat varieties classified as resistant in the United States were susceptible to stripe rust collected in Germany. The studies reported in the present paper indicate that the physiologic forms prevalent in Canada are different from those commonly present in Europe. All Canadian collections of this rust have been identified as either form 8 or form 13. The former has been found in Europe but the latter, which has not been reported outside of America, appears to be by far the most common form in Canada.

Acknowledgments

The writers wish to express their indebtedness to Dr. Ruth F. Allen, Berkeley, California, Miss M. Cudmore, Cambridge, England, and Dr. W. M. Bever, Moscow, Idaho, for cultures of *P. glumarum*; and to Dr. G. Gassner and Dr. W. Straib, Brunswick, Germany, for pure cultures of two physiologic forms as well as for seed of their differential wheat varieties. They are also indebted to Dr. A. Scheibe, formerly of Berlin-Dahlem, Germany, for seed of his differential wheat varieties.

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BUNODERINA EUCALIAE GEN. ET SP. NOV., A NEW PAPILLOSE ALLOCREADIIDAE FROM THE STICKLEBACK¹

By M. J. MILLER²

Abstract

A new species of trematode is described from the intestine of the stickleback (*Eucalia inconstans*), and referred to a new genus.

In the last week of October and in early November, 1935, a number of brook sticklebacks (*Eucalia inconstans*) were examined and found to harbor a trematode, the consequent study of which showed it to be, as yet, undescribed. This fluke belongs to the family Allocreadiidae, and more specifically to that group known as the papillose Allocreadiidae. The characteristics revealed by this trematode necessitate the formation of a new genus for which the name *Bunoderina* is proposed, and for the species, *B. eucaliae* is proposed.

The specimens studied were fixed in Schaudinn's solution, stained in alum carmine and mounted in balsam. It was found that specimens in tap water passed out their eggs; these specimens were useful for determining the form of the uterus, but could not be satisfactorily fixed. Considerable difficulty was encountered in fixing the trematodes in a normal position. Satisfactory results were obtained by placing the entire intestine of the fish in hot fixative, and then dissecting out the trematodes.

This species is found attached by its suckers or free in the intestine of the sticklebacks.

Specific Diagnosis

Body thick and muscular, almost circular in cross section, 0.83 to 1.06 mm. long and 0.31 to 0.35 mm. wide. One sexually immature specimen measured 0.56 mm. in length. Body widest at the middle and narrowing off at both ends. Cuticle smooth. Suckers comparatively large, ventral sucker larger than the oral sucker. Pharynx well developed. Oesophagus long, S-shaped unless the anterior end of body is extended; it bifurcates at a point slightly anterior to the acetabulum. Intestinal crura wide and contractile, extending down into the third quarter of the body, dorsal to and slightly overlapping the vitellaria.

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² Graduate Student.

Testes sub-circular, usually oblique but may be side by side, situated in the third quarter of the body. Vasa efferentia enter the cirrus sac separately. Cirrus sac small and relatively broad, overlapping the ventral sucker to about one-third its diameter; it contains a seminal vesicle and a cirrus. Finer morphology of cirrus sac was not studied.

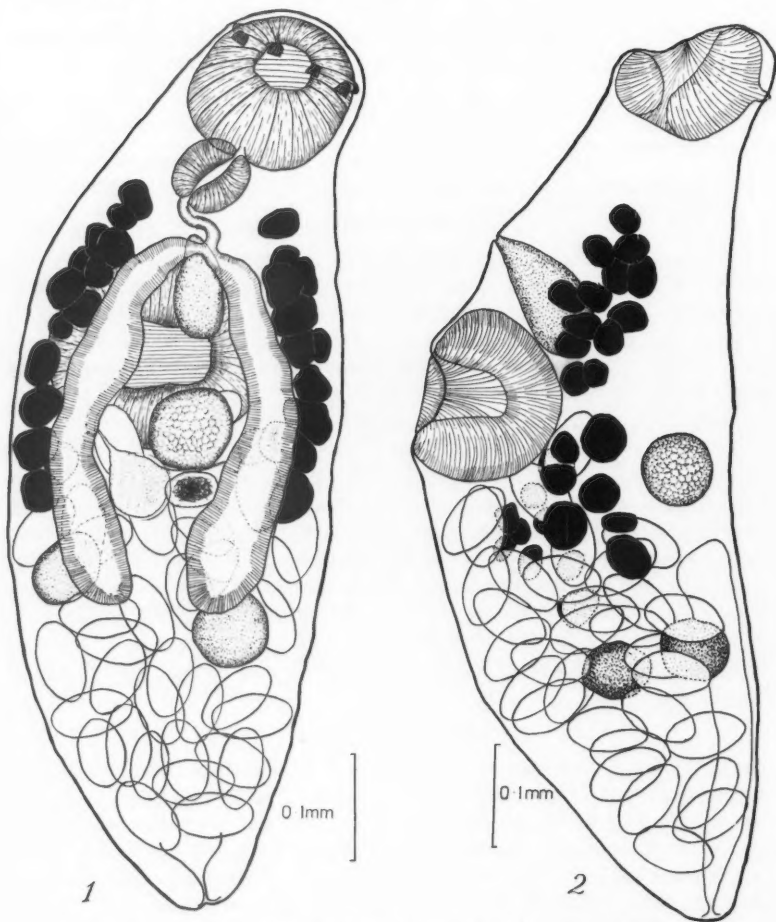


FIG. 1. *Bunoderina eucaliae* gen. et sp. nov. 1. Dorsal view. 2. Lateral view.

Ovary circular, dorsal to the posterior part of the acetabulum. Spermatheca large, directly caudad of the ovary. Laurer's canal with bulbous base. An oötype or shell gland could not be detected. Uterus a convoluted tube filling the posterior part of the body. Vitellaria composed of comparatively

few, large follicles, extending from a short distance anterior of the acetabulum to the posterior portion of the middle third of the body, terminating just anterior of the end of the intestinal crura.

Excretory vesicle a bladder-like structure which may extend forward as far as the acetabulum.

Eggs ovoid, 0.07 to 0.83 mm. long by 0.044 to 0.047 mm. wide, light brown in color and containing active miracidia when deposited.

Host: Brook stickleback (*Eucalia inconstans*).

Location: Small intestine.

Locality: Drainage canal, Jacques Cartier Co., Que., Canada.

Discussion

The description of *Bunoderina eucaliae* as given agrees with all the specimens examined. There is, however, a variation in shape of body that corresponds with age. In the older trematodes the posterior part of the body becomes wider with the increasing number of eggs; it does not however, become sacculate as in *Bunodera sacculata*.

B. eucaliae differs from other species of the papillose Allocreadiidae in the form of the uterus and the reduced number of vitelline follicles. As has been stated, its uterus is a narrow convoluted tube, filling the posterior portion of the body. Nowhere else in the papillose Allocreadiidae does this type of uterus occur. In *Crepidostomum* and *Megalogonia* the uterus is a narrow tube, but it is characteristically short, with few, if any, convolutions. *Bunodera* has the ascending ramus of the uterus expanding into a uterine sac. The writer therefore considers the form of the uterus to be a character of generic importance, and thinks it justifiable to create a new genus with *B. eucaliae* as the type and only species.

Generic Diagnosis

Allocreadiidae, with six oral papillae, four dorsal and two ventro-lateral. Ventral sucker larger than the oral sucker. Testes sub-circular, obliquely arranged to nearly opposite, situated in the third quarter of the body. Uterus a narrow convoluted tube, filling the posterior part of the body. Vitelline follicles reduced in number.

Holotype Specimen in Helminthological collection, Institute of Parasitology, McGill University, Macdonald College, P.Q., Canada.

Paratype deposited at Helminthological collection, Department of Zoology, University of Illinois, Urbana, Illinois, U.S.A.

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A GRAPHICAL METHOD FOR THE RAPID ESTIMATION OF THE STANDARD DEVIATION¹

BY R. HOLCOMB² AND DAROL K. FROMAN³

Abstract

A graphical method, based upon Galton's "ogive" curve, that may be used for estimating the various criteria of variability including the standard deviation, is described. Curves of this type are more readily adaptable to tests for normality of distribution than are the customary frequency histograms, especially with a limited number of observational data.

The purpose of this paper is to present a simple graphical method for the estimation of standard deviation and the degree of normality of a distribution. This method may be found useful by those who have not available the facilities of a statistical laboratory. It is essentially a short-cut, facilitating the analysis of observational data with special reference to the variation within a group, as measured by the standard deviation and the probable errors of averages. The same graphical method may also serve to illustrate variation, both absolute and relative, as when applied either to one or to more groups of observations.

It is currently popular to illustrate variation by means of frequency histograms. For such diagrams, it is necessary to group the data, and if the number of observations is small, either the variation within a group is so large, or the number of groups is so small, that it is difficult to estimate whether the distribution approaches normality. In this case estimates of such quantities as standard deviation cannot be made from the graph. Even for large numbers of observations little more may be obtained from the diagram than the position of the mode, the two extremes, and the probable position of the arithmetic mean.

The graphical method given here can be described best by means of an example. Table I gives the percentage of fat contained in the thigh muscles of 139 chickens. The data are arranged in order of increasing percentage and numbered in order from 1 to 139. If then, the percentage of fat be plotted against the number of the observation, we obtain the distribution shown in Fig. 2. Curves of this form were first proposed by Sir Francis Galton (1) in 1875, but little use has since been made of them. Since each observation appears as a plotted point, the form of the distribution is made directly evident, even for a small number of observations where a frequency histogram might be quite useless. As Galton pointed out, the median, the quartiles and the deciles may be read directly from this graph. All of these points are of value in describing the distribution of the observed values.

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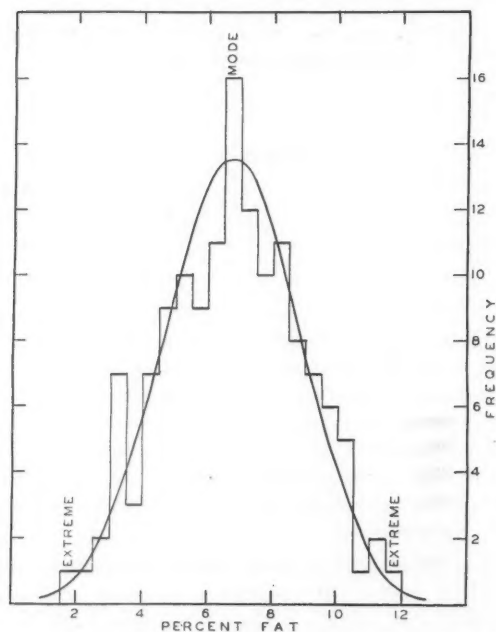


FIG. 1. Frequency histogram showing distribution of the fat content of thigh muscles of the domestic fowl (Cf. Fig. 2 showing the same data arranged as an ogive curve).

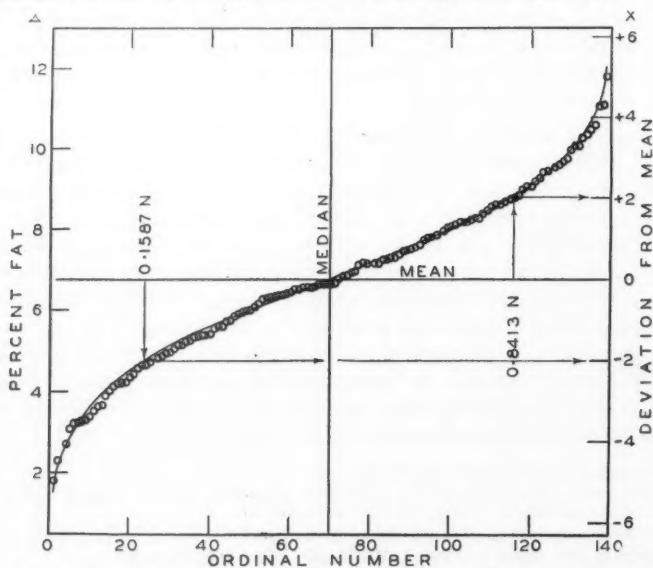


FIG. 2. Graphical approximation of the standard deviation from an ogive curve.

TABLE I
THE FAT CONTENT OF THE THIGH MUSCLES OF CHICKENS

No.	% fat	No.	% fat	No.	% fat	No.	% fat
1	1.86	36	5.33	71	6.69	106	8.24
	2.36		5.34		6.78		8.26
	2.58		5.37		6.85		8.38
	2.76		5.38		6.86		8.42
5	3.12	40	5.41	75	6.92	110	8.56
	3.25		5.57		6.99		8.59
	3.27		5.61		7.12		8.61
	3.31		5.61		7.14		8.65
	3.32		5.75		7.14		8.70
10	3.42	45	5.76	80	7.14	115	8.72
	3.45		5.85		7.15		8.77
	3.63		5.92		7.15		8.83
	3.68		5.96		7.23		9.00
	3.92		5.97		7.25		9.05
15	4.03	50	6.01	85	7.29	120	9.07
	4.15		6.18		7.30		9.16
	4.21		6.29		7.37		9.26
	4.21		6.32		7.43		9.40
	4.23		6.33		7.50		9.40
20	4.39	55	6.34	90	7.50	125	9.50
	4.47		6.38		7.58		9.51
	4.60		6.39		7.61		9.56
	4.67		6.42		7.72		9.65
	4.67		6.44		7.77		9.71
25	4.68	60	6.47	95	7.79	130	9.98
	4.79		6.51		7.81		10.03
	4.85		6.52		7.89		10.05
	4.87		6.56		7.93		10.23
	4.95		6.57		8.02		10.31
30	4.98	65	6.57	100	8.09	135	10.43
	5.06		6.58		8.10		10.51
	5.16		6.64		8.13		11.01
	5.17		6.64		8.13		11.03
	5.22		6.65		8.17		11.79
35	5.24	70	6.66	105	8.19	139	

By use of the deciles the arithmetic average may be rapidly approximated, for it is evident that these deciles should be regularly spaced about the average, if the distribution is normal. The differences of the deciles from the median are averaged (Table II) for the corresponding pairs, and a set of corrected "medians" obtained by adding these averages to the deciles. The grand average of these corrected "medians" is then taken as the average of the entire group. For the data used here, the estimated average is found to be 6.75, which agrees perfectly with the calculated arithmetic average.

In Fig. 2, the mean value for the percentage of fat may now be drawn, and the scale (X) may now be changed to read deviations from the mean (x -scale). It will be observed that the points in Fig. 2 appear to follow a

TABLE II
THE APPROXIMATION OF THE ARITHMETIC AVERAGE BY THE USE OF DECILES

Decile number	Observ. number	Decile value	Differences from median			
1	14	3.92	0.28	1.05	1.79	2.74
2	28	4.87				
3	42	5.61				
4	56	6.38				
5	70	6.66	0.59	1.27	1.95	2.85
6	84	7.25				
7	98	7.93				
8	112	8.61				
9	126	9.51				
Sums			0.87	2.32	3.74	5.59
Mean			0.43	1.16	1.92	2.80
Corrected median			6.81	6.77	6.73	6.71
Grand average			6.75			

smooth curve, starting steeply, gradually flattening out across the centre, and rising steeply again towards the end. It can be shown that, for a perfectly normal distribution, the relation which fits such an arrangement is given by the equation,

$$n = \frac{N}{2} \pm \frac{N}{2\sqrt{\pi}} \int_0^{\frac{x}{\sqrt{2}\sigma}} e^{-\frac{t^2}{2}} dt \cdot d\left(\frac{x}{\sqrt{2}\sigma}\right)$$

where N is the total number of observations, σ is the standard deviation, and x is the deviation from the mean of the n^{th} observation. The number n is the serial number of the observation in the arranged order.

The curve for the data illustrated here, where N is equal to 139 and σ , calculated from residuals, is equal to 2.06, has been superimposed upon the points. It appears to fit the data remarkably well.

The general properties of curves of this family are shown in Fig. 3, where six curves are given for values of σ from 1 to 6. When σ is equal to zero, or no variation is shown in the group, all values would lie along the mean line. As the degree of variation becomes larger or σ increases, the curves cross the mean line at greater and greater angles, at the same time becoming more nearly straight lines. A special point of interest is that at any point along the N -axis, the distance of the curve from this axis is directly proportional to the standard deviation. As shown in Fig. 3, the ratios of the distances of the curves from the N -axis are as 1 : 2 : 3 : 4 : 5 : 6. This leads directly to the method for the approximation of the standard deviation.

For example, when,

if $x/\sigma = 0.5$, then $n = N/2 \pm 0.1918N$,

if $x/\sigma = 1.0$, then $n = N/2 \pm 0.3413N$,

and if $x/\sigma = 1.5$, then $n = N/2 \pm 0.4332N$.

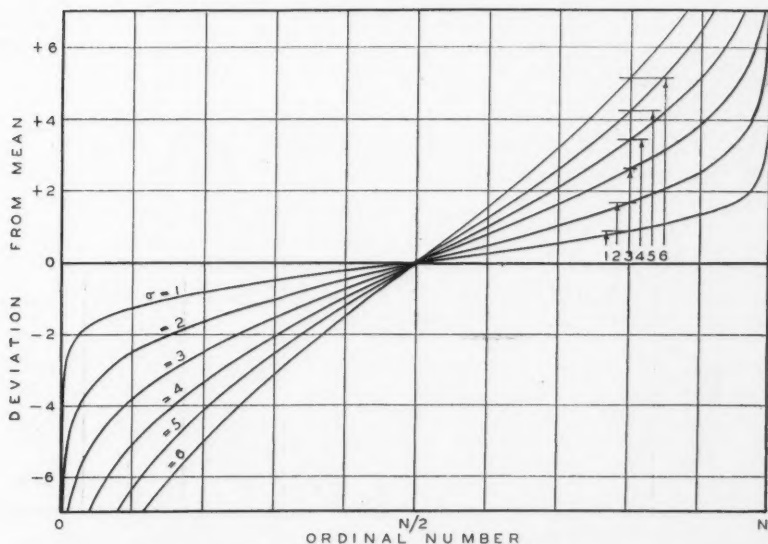


FIG. 3. Family of ogive curves for several standard deviations.

All that is required is to read from the graph the values of x corresponding to the six values of n given in the right-hand equations above. Six approximations of σ are obtained, the average of which is assumed to be a good estimate. The detailed work is given in Table III.

The method is shown graphically in Fig. 2. If the curve is fairly symmetrical about the mean and median, a fair estimate of the value of σ can be obtained by reading only two values of x at $n = N/2 \pm 0.3413N$. The accuracy of the estimate is improved, in general, by increasing the number of approximations. Perpendiculars have been erected from the points 0.1587N (22) and 0.8413N

TABLE III
THE APPROXIMATION OF THE STANDARD DEVIATION

x/σ	n	x	σ
0.5	$\nabla 0.3083N$ (42.9)	1.14	2.28
0.5	$\nabla 0.6917N$ (96.1)	1.07	2.14
1.0	$\nabla 0.1587N$ (22.0)	2.15	2.15
1.0	$\nabla 0.8413N$ (117)	2.07	2.07
1.5	$\nabla 0.0668N$ (9.3)	3.40	2.26
1.5	$\nabla 0.9332N$ (130)	3.15	2.10
Average			2.16
Calculated			2.06
Error			5%

TABLE IV
VALUES OF THE PROBABILITY INTEGRAL FOR RATIOS OF x/σ^*

x/σ	$I = \frac{1}{2\sqrt{\pi}} \int_0^{\frac{x}{\sqrt{2}\sigma}} e^{-\frac{t^2}{2}} dt$	$\log_{10} I$
0.25	0.0988	$\bar{2}.99476$
0.50	0.1917	$\bar{1}.28262$
0.75	0.2732	$\bar{1}.43648$
1.0	0.3413	$\bar{1}.53314$
1.5	0.4332	$\bar{1}.63669$
2.0	0.4772	$\bar{1}.67870$
2.5	0.4937	$\bar{1}.69346$
3.0	0.4986	$\bar{1}.69801$
4.0	0.4999	$\bar{1}.69888$

*For table from $x/\sigma = 0.00$ to 4.24 by units of 0.01 see *Medical Biometrics*, by Raymond Pearl, Philadelphia, 1923.

(117). The point of intersections, when carried over to the x -scale, gives the value of the standard deviation, since at these two values of n , x/σ is equal to 1.0.

In Table IV the values of the integral are given for various values of the ratio x/σ from which curves to fit any data may be rapidly computed. The data for the fitting of the curve in Fig. 2 is given in Table V.

TABLE V
DETAILS OF CURVE-FITTING FOR FIG. 2

x/σ	$\frac{1}{2\sqrt{\pi}} \int_0^{\frac{x}{\sqrt{2}\sigma}} e^{-\frac{x^2}{2\sigma^2}} d\left(\frac{x}{\sqrt{2}\sigma}\right)$	Integral times N	$+N/2$	$-N/2$	x
0.25	0.0988	13.7	83.2	55.8	0.51
0.50	0.1917	26.6	96.1	42.9	1.03
0.75	0.2723	38.0	107.5	31.5	1.54
1.0	0.3413	47.4	116.9	22.1	2.06
1.5	0.4332	60.2	129.7	9.3	2.09
2.0	0.4772	66.4	135.9	3.1	4.12
2.5	0.4937	68.6	138.1	0.9	5.15

The value of the method lies in the ease with which an approximation to σ may be obtained from an immediate plot of the data, and in the usefulness of such a graph for judging the skewness of the deviations for small numbers of observations. With very little practice it is possible to tell from such curves whether the distribution approaches normality sufficiently to apply a more rigorous statistical treatment.

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